ORNIS SVECICA 6:89–96, 1996

The timing of post-juvenile moult and fuel deposition in relation to the onset of autumn migration in Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus*

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Abstract

The extent of post-juvenile moult and fuel deposition prior to migration in Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *A. schoenobaenus* were analysed using 11 years ringing data from Lake Kvismaren in South Central Sweden. Re-trap data showed that Reed Warblers acquired their first winter plumage in 34 days, compared to 22 days in Sedge Warblers. The moult pattern of the two species differed due to Sedge Warblers only undertaking a fill-in moult of bare body areas. Fuel deposition rates for the two species were similar, 0.38 g/day for Reed Warblers and 0.34 g/day for Sedge Warblers. The estimated average fuel stores at departure from Lake Kvismaren differed, with Reed Warblers found to leave with a fuel store of 21 % (in relation to lean body mass) compared to 6.2 % in Sedge Warblers. The median date of departure from Lake Kvismaren was estimated to 30 August for Reed Warblers and 12 August for Sedge Warblers. The earlier departure of Sedge Warblers, with smaller fuel stores, may reflect different migration strategies between the species.

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Received 6 February 1996, Accepted 7 July 1996, Editor: Å. Lindström

Introduction

Most long-distance migrants at northern latitudes remain for only a brief period of time on the breeding grounds. Because the time schedule is compressed, a first year bird does not only need to reach independence quickly but also to prepare for migration by attaining fully grown wing and tail feathers and a body plumage of good quality as fast as possible (Heinroth & Heinroth 1924–6, Ginn & Melville 1983). Energy stores for flight, comprised of both fat and fat-free tissue (cf. Lindström & Piersma 1993), are also required before migration can start (Blem 1980). In most species the first set of body contour feathers are weak and loose in structure and are renewed during the post-juvenile body moult (Ginn & Melville 1983, Jenni & Winkler 1994). Some species of migratory birds apparently try to minimise the time spent on migration (Lindström & Alerstam 1992, Fransson 1995). If the time period used for post-juvenile moult is of short duration, departure from natal areas could take place earlier, thus reducing time pressure during migration. The present study compares the post-juvenile moult and pre-migratory fuel deposition, mainly the deposition of visible subcutaneous fat, in Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus* prior to autumn migration from Lake Kvismaren.

Materials and methods

I have analysed data collected during standardised ringing activity at Kvismare Bird Observatory in South Central Sweden (59°11'N, 15°24'E) from 1984 to 1994. A total of 9086 juvenile Reed Warblers and 4710 juvenile Sedge Warblers were examined at Vallen at Västra Fågelsjön and at Banvallen at Rysjön 3 km away. Both localities are eutrophic inland lakes surrounded by dense reedbeds and bushes and situated in a farmland area. Deciduous forest borders upon Lake Rysjön where birds were mist-netted. In this analysis data from the two localities have been pooled since the average wing length did not differ between the two ringing sites. The capture season covered the end of June to 30 September with only birds caught between dawn and noon analysed in order to minimise any diurnal body mass fluctuations.

A total of 1143 Reed Warblers and 444 Sedge

Warblers were retrapped and reexamined at least once one day or more after ringing. The majority were recaught at the ringing site but some at other places in the Kvismare area.

On all birds body mass, visible body fat load and juvenile moult score were taken. There were indications that Sedge Warblers did not replace natal body feathers during post-juvenile moult (Bensch & Lindström 1992) but due to lack of alternative scales, both species were assessed for post-juvenile moult using the same scoring system (see Fig. 2). Since the aim of this study was to estimate the time period from juvenile to first winter plumage and departure time, the scale was considered accurate for both species. Ageing followed Svensson (1984) and Karlsson et al. (1988). Birds were weighed using a spring balance to an accuracy of 0.1 g. Post-juvenile moult was scored following the scale developed by Bensch & Lindström (1992) for Willow Warblers *Phylloscopus trochilus*. Moult stage 1 (M1) represents a bird with the growth of primaries not yet completed. Moult stage 2 (M2) are birds in light moult and stage 3 and 4 (M3 and M4) are birds in heavy moult (growing feathers all over the body). Stage 5 (M5) represents almost completed moult and stage 6 (M6) a bird in first winter plumage. The classification of subcutaneous fat follows the scale of Pettersson & Hasselquist (1985), from 0 indicating a bird with no fat through 6 indicating a large amount of fat present. Ringers regularly compared their estimates of moult extent and fat score.

The body mass at departure and departure date from the Kvismare area were estimated from the fattest quartile of the birds (see Alerstam & Lindström 1990) in late and completed moult (M5 and M6). By analysing the fattest birds, instead of the heaviest, bias caused by size differences (c.f. Ellegren & Fransson 1992) was minimised. To select which individuals to include in the estimation, sampling was done with help of the randomising program in Systat for Windows, version 5.

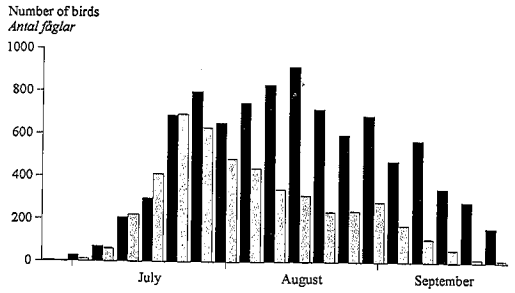

Fig. 1. The catching pattern of Reed Warblers (black) and Sedge Warblers (grey) in international 5-day periods. Data for periods 35/36 and periods 54/55 respectively were pooled due to small sample sizes.

Den totala fångstens fördelning över säsongen av rörsångare (svart) och sävsångare (grått) enligt internationella 5-dagarsperioder. De första och sista två 5-dagarsperioderna, perioderna 35/36 respektive 54/55, har slagits samman på grund av liten fångst.

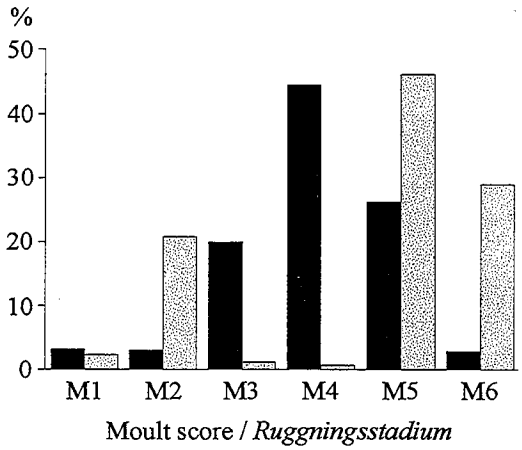

Fig. 2. The proportion of birds in different moult scores in the total catch of Reed Warblers (black) and Sedge Warblers (grey).

Den procentuella fördelningen av fåglar i olika ruggningsstadier i den totala fångsten av rörsångare (svart) och sävsångare (grått).

Results

Catching pattern

Juvenile Reed Warbler numbers reached their peak in the middle of August with 10.1 % of birds trapped between 14–18 August (Fig. 1). The peak for Sedge Warblers occurred during the second part of July with 14.7 % of the birds caught between 20–24 July (Fig. 1). Median trapping dates were 14 August for Reed Warblers and 2 August for Sedge Warblers.

Post-juvenile moult

The percentage of birds in each moult stage differed between the two species with Reed Warblers showing a single peak at M4, whereas a small peak at M2 and a large peak at M5 were present in Sedge Warblers (Fig. 2). Very few Sedge Warblers in M3 and M4 were caught. Reed Warblers were first caught in first winter plumage (M6) in early August

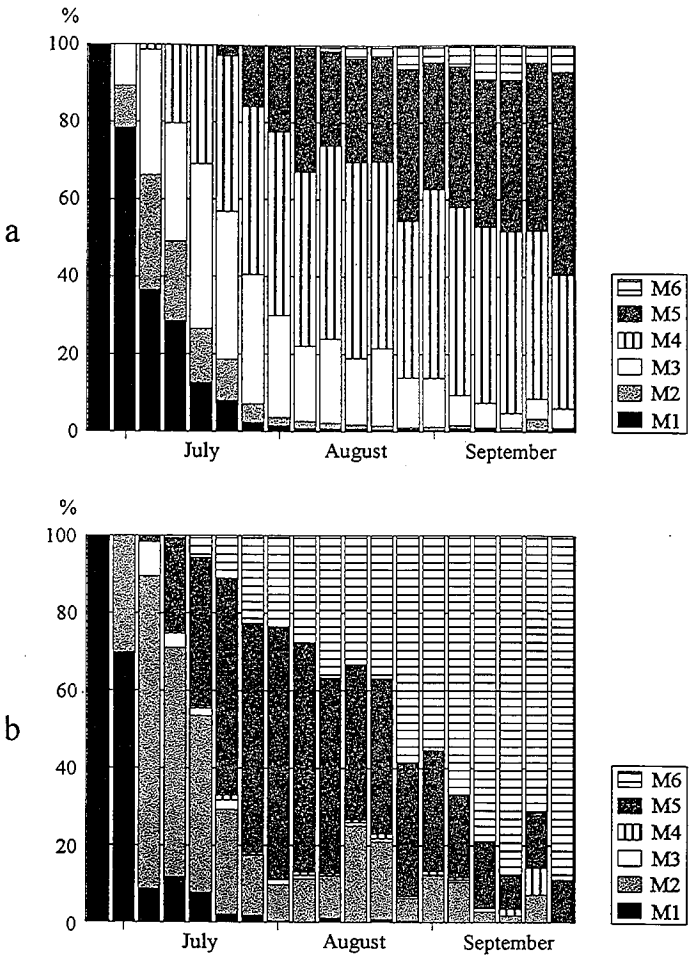

Fig. 3. The proportion of birds in different moult scores within each 5-day period for Reed Warblers (a) and Sedge Warblers (b).

Den procentuella fördelningen av fåglar i olika ruggningsstadier under säsongen för rörsångare (a) och sävsångare (b).

(Fig. 3a) whereas the earliest Sedge Warblers caught in first winter plumage occurred in the middle of July (Fig. 3b). Reed Warblers in early moult (M1) were present during a longer period than Sedge Warblers, and the catch of Sedge Warblers was dominated by birds in complete or almost complete first winter plumage (M5 and M6) from the second part of July. By the end of September the mean moult score in the total catch of Reed Warblers was 4.6 (n=163) compared to 5.9 (n=9) for Sedge Warblers.

The within year difference between species showed that the median date of Reed Warblers in early moult (M1) was on average 5 days later (s.d.=2.8) than that of Sedge Warblers. The average difference in median dates for complete first winter plumage (M6) was 19 days (s.d.=11.1 days), giving a 14 days shorter moult period for Sedge Warblers. The average moult period calculated from the mean time difference between median dates from M1 to M6 for each year gives a moult period of 48 days (s.d.=6.2) for Reed Warblers and 31 days (s.d.=3.8) for Sedge Warblers, a difference of 17 days. Retrapped birds showed that the post-juvenile moult period for Reed Warblers lasted 34 days and for Sedge Warblers 22 days (Table 1), a time difference of 12 days.

Fuel deposition

The average lean body mass calculated from birds in first winter plumage with fat score 0 was 10.78 g for Reed Warblers (s.d.=0.44, n=11) and 10.75 g for Sedge Warblers (s.d.=0.56, n=314). The patterns of visible body fat deposition were similar for the two species (Figs 4a and b).

Table 1. The average time period between post-juvenile moult scores for Reed Warblers and Sedge Warblers at Lake Kvismaren. Calculations were based on re-trapped birds.

Genomsnittlig tid mellan olika ruggningsstadier för rörsångare och sävsångare vid Kvismaren. Beräkningarna bygger på återfångade fåglar.

Moult score interval *Ruggningsintervall*	Reed Warbler *Rörsångare* days *dagar*	n	Sedge Warbler *Sävsångare* days *dagar*	n
1–2	6.7	7	8.9	12
2–3	8.3	32		
3–4	7.3	119		
4–5	6.7	128	7.2*	29
5–6	5.3	32	5.5	72
1–6	34.3		21.6	

* Moult score 2–5 *Ruggningsintervall 2–5*

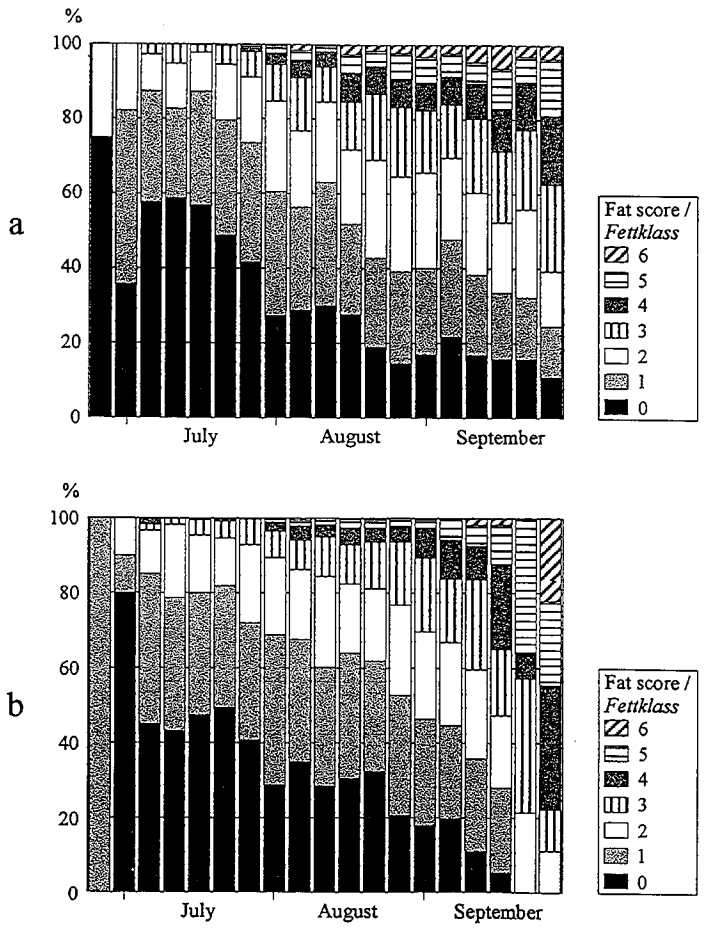

Fig. 4. The proportion of birds with different fat scores in 5-day periods for Reed Warblers (a) and Sedge Warblers (b).

Den procentuella fördelningen av fåglar i olika fettklasser under säsongen för rörsångare (a) och sävsångare (b).

A total of 54.1 % of all Reed Warblers trapped when in first winter plumage (n=266) showed a fat score of 5 or 6, compared to only 4.3 % of Sedge Warblers (n=1349). Over 92 % of birds, of both species, with a fat score of 6 had a complete or almost complete first winter plumage. The actual fuel reserves of birds with a fat score of 6 (calculated from birds in first winter plumage as the difference between the estimated lean body mass and the body mass in fat score 6) were higher for Reed Warblers, 3.49 g (S.D.=1.23 g, n=71), than for Sedge Warblers, 2.52 g (S.D.=0.97 g, n=9). Each species showed a strong positive relationship between body mass and fat score (Reed Warbler r^2=0.542, b=0.64, p<0.001, n=264; Sedge Warbler r^2=0.296, b=0.30, p<0.001, n=1333) when in first winter plumage. However, the mean body mass gain per fat score (0.64 g and 0.30 g, respectively) differed between the two species (t=25.6, p<0.001).

Only retrapped birds were used to calculate fuel deposition rates and to minimise the inclusion of any individuals that not yet had started to deposit fuel for migration, only rates higher than 0.2 g/day were used. This gave a mean fuel deposition rate of 0.38 g/day for Reed Warblers (max. 1.03 g/day over a 3 day period, s.d.=0.17, n=104) and 0.34 g/day for Sedge Warblers (max. 1.10 g/day over a 1 day period, s.d.=0.20, n=21).

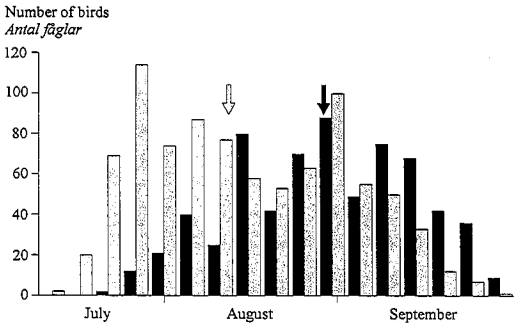

Fig. 5. The catching pattern of the 25 % fattest birds in late moult or first winter plumage (M5 and M6) for Reed Warblers (black) and Sedge Warblers (grey) in international 5-day periods. Arrows indicate median trapping dates (Reed Warbler 30 August, Sedge Warbler 12 August) which are supposed to reflect median departure dates.

Fångstens fördelning över säsongen av de 25 % fetaste fåglarna i nästan eller helt komplett första vinterdräkt (M5 och M6) för rörsångare (svart) och sävsångare (grått). Pilarna anger mediandatum för fångst, vilket anses överensstämma med datum för bortflyttning (rörsångare 30 augusti, sävsångare 12 augusti).

Onset of migration

Reed Warblers departed with an average body mass of 13.04 g (s.d.=1.18, n=659), and a fat score of 4.9. This is equal to a fuel reserve of 21.0 % in relation to lean body mass and a projected flight distance of 757 km in still air conditions (calculated according to Program 1, Pennycuick 1989). Sedge Warblers departed with an average body mass of 11.42 g (s.d.=0.83, n=875) and a fat score of 3.0, giving an average fuel reserve of 6.2 % in relation to lean body mass and a projected flight distance of 240 km. With the estimated deposition rates it would take on average 6 days for Reed Warblers and 2 days for Sedge Warblers to accumulate enough fuel to commence migration.

The median departure dates, calculated as the median dates of the fattest quartile of birds in late moult or first winter plumage (M5 and M6), was 30 August for Reed Warblers (n=659) and 12 August for Sedge Warblers (n=875)(Fig. 5).

Discussion

From retrapped Reed Warblers in this study, post-juvenile moult was estimated to take 34 days while the same value was 48 days according to median capture dates of the whole population. Similarly, Sedge Warblers acquired their first winter plumage in 22 days or 31 days, respectively. It is probable that the retrap estimate gives a more accurate value. By using the median trapping dates the estimate could be influenced by migrating birds from populations further north which may have a later moult season than birds born at Kvismaren. This would result in a protracted capture period of late moult stages at Kvismaren which would affect median capture dates. However, the difference in time period between species is similar irrespective of the method used.

The duration of post-juvenile moult in Reed Warblers based on retrapped birds was similar to other warbler species. For instance Norman (1990) estimated this in England to be 30 days for Garden Warblers *Sylvia borin*, 35 days for Lesser Whitethroats *Sylvia curruca* and 40 days for Whitethroats *Sylvia communis*.

The pattern of the post-juvenile moult differed markedly between the two species at Lake Kvismaren. While Reed Warblers showed similar moult sequence to Willow Warblers (Bensch & Lindström 1992) Sedge Warblers appeared not to undertake any replacement moult. The Sedge Warblers seemed to acquire their first winter plumage with only filling in

of bare body areas. Consequently, no heavy moult stages should be recorded, which was also the case in this study. Müller (1981) mentions that juvenile Savi's Warblers *Locustella luscinoides* follow this trait. In both Sedge and Savi's Warblers juvenile plumages are similar in texture to the adult plumages and can be retained until first winter moult (Heinroth & Heinroth 1924–6). Also Bensch & Lindström (1992) state that the Sedge Warbler, as well as the Marsh Warbler *Acrocephalus palustris* and the Great Reed Warbler *A. arundinaceus*, may only undertake a fill-in moult of bare body areas. This moult pattern also occurs in Aquatic Warblers *A. paludicola*, Icterine Warblers *Hippolais icterina*, Melodious Warblers *H. polyglotta* and among many species in the genus *Locustella* (Cramp 1992). It seems obvious that a separate moult scale for species attaining first winter plumage in this manner is needed.

The fuel deposition rates of the two species were fairly similar at Kvismaren, 0.38 g/day for Reed Warblers and 0.34 g/day for Sedge Warblers. For juvenile Reed Warblers the deposition rate at Kvismaren was higher than previous estimated values. For instance Gladwin (1963) showed this rate to be 0.28 g/day in England and Bibby & Green (1981) gave 0.25 g/day in Portugal in autumn. For Sedge Warblers on autumn migration Bibby & Green (1981) estimated the rate at 0.32 g/day in England and 0.42 g/day in France. In a second study Bibby et al. (1976) estimated rates of 0.49 g/day and 0.58 g/day in England in good years whereas Gladwin (1963) calculated the rate of fat deposition at 0.38 g/day for British Sedge Warblers in autumn.

The average increase in body mass per fat score was much higher in Reed Warblers, 0.64 g/fat score, than in Sedge Warblers, 0.30 g/fat score. This suggests that Reed Warblers with a fat score of 6 have a much larger energy store than Sedge Warblers with the same fat score. In fact, this increase per fat score of Reed Warblers is similar to that of Robins *Erithacus rubecula*, 0.67–0.85 g/fat score, whereas the Sedge Warbler shows an increase similar to the one in Goldcrests *Regulus regulus*, i.e. 0.22–0.25 g/fat score (Pettersson & Hasselqvist 1985).

The estimated energy store for Reed Warblers gives sufficient fuel for non-stop flight from Lake Kvismaren to northern Germany (757 km) and for Sedge Warblers to Sävsjö, Småland in South Sweden (240 km). Both species are nocturnal migrants and as data were collected in the mornings a slight under-estimate of the fuel stores are possible (Baggott 1975, Aidley & Wilkinson 1987). The decreasing probability of catching heavier birds (Bibby et al. 1976) may also cause under-estimates in fuel stores.

The median departure dates from Kvismaren were estimated to 30 August for Reed Warblers and 12 August for Sedge Warblers, a time difference at departure of 18 days. This time difference, as well as the smaller fuel stores of Sedge Warblers at departure, is in accordance with the results of Nielsen & Rhönnstad (1996) in their study of Reed and Sedge Warblers at Kvismaren. In Wales the peak passage of both Reed and Sedge Warblers on autumn migration occurs within a week in early August (Ormerod 1990) and in southern England juveniles of both species peak within 10 days in late August (Bibby & Green 1981).

The smaller fuel stores of Sedge Warblers and the earlier departure than Reed Warblers indicates that the two species follow different migration strategies. An interesting point, however, is that Sedge Warblers at Falsterbo, in southernmost Sweden, leave Sweden on autumn migration a few days *later* than Reed Warblers, but still with smaller fuel stores (Falsterbo Bird Observatory, pers. comm.).

Although it is obvious that the two species differ in several important aspects it is not yet possible to draw any general conclusions about the underlying reasons for and consequences of this. Further analysing of data from other ringing sites in Sweden and along the autumn migration routes in Europe may clarify the situation.

Acknowledgements

My thanks are due to all ringers and assistants at Kvismare Bird Observatory throughout the years without whom this study would not have been possible. I am also indebted to Bo Nielsen for giving me access to the Kvismare data files. I specially want to thank the Department of Zoology, Stockholm University, and Thord Fransson for advice on data processing, translation of German papers and valuable discussions over this manuscript. The manuscript also benefited from valuable comments from Christer Wiklund, Hans Temrin, Åke Lindström and two anonymous referees. This is report no. 90 from Kvismare Bird Observatory.

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Sammanfattning

Tidsmässiga aspekter på ruggning och bränsleupplagring hos juvenila rörsångare Acrocephalus scirpaceus *och sävsångare* A. schoenobaenus *inför höstflyttningen*

Vid ringmärkning av fåglar har det noterats att ungfågelruggningen, bytet av fjäderdräkt från juvenil dräkt till första vinterdräkten, skiljer sig åt mellan rörsångare och sävsångare. Båda arterna är långdistansflyttare och kan antas vara mer eller mindre tidspressade på häckningsplatserna. I den här studien har jag undersökt om ruggningsmönstren hos rör- och sävsångare skiljer sig åt samt hur detta påverkar tidpunkten för höstflyttningen. Jag har även jämfört de båda arternas bränsleupplagring, framförallt av synligt underhudsfett, och bränslereserv inför bortflyttningen.

Materialet består av ringmärkningsdata från den ordinarie ringmärkningsverksamheten vid Kvismare fågelstation (59°11'N 15°24'E) åren 1984–1994. Data från två märkplatser, Vallen vid Västra Fågelsjön och Banvallen vid Rysjön, har använts. Totalt ingår 9086 juvenila rörsångare och 4710 juvenila sävsångare i studien. Av dessa har 1143 rörsångare och 444 sävsångare återfångats under samma säsong, minst en dag efter ringmärkning. Ruggningen är bedömd enligt en skala från 1–6, där 1 (M1) är en individ utan fullständigt utvuxna handpennor medan 6 (M6) är en färdigruggad fågel i första vinterdräkt (Bensch & Lindström 1992). Fettupplagringen är bedömd efter en skala från 0–6 där fettklass 0 motsvarar en fettfri individ och fettklass 6 en mycket fet fågel (Pettersson & Hasselqvist 1985).

Fångstens fördelning över säsongen var liknande för båda arterna (Fig.1). Mediandatum för rörsångarfångsten var 14 augusti och för sävsångarfångsten den 2 augusti. Fångstens fördelning på olika ruggningsstadier skilde sig dock åt (Fig. 2). De flesta rörsångarna fångades i intensiv ruggning (M4) medan de flesta sävsångarna fångades så gott som färdigruggade (M5). Mycket få sävsångare bedömdes vara i intensiv ruggning (M3 eller M4) vid fångsttillfället. De olika ruggningsstadiernas fördelning över säsongen skilde sig också åt mellan de två arterna (Fig. 3a och b). Rörsångare fångades i stadie 1 under längre tid är sävsångare. Hos rörsångare dominerade de intensiva ruggningsstadierna (M3 och M4) från mitten av juli till början av september. Fångsten av

sävsångare dominerades av fåglar i komplett eller så gott som komplett första vinterdräkt redan från slutet av juli.

Mediandatum för fångsten av rörsångare i ruggningsstadie 1 (M1) låg i genomsnitt 5 dagar senare än för sävsångare. Hos färdigruggade fåglar (M6) hade skillnaden ökat till 19 dagar, vilket innebär att sävsångaren skulle rugga på 14 dagar kortare tid än rörsångaren. Ruggningstidens längd, beräknat efter mediandatum för fångsten i olika ruggningsstadier, blev 48 dagar för rörsångare och 31 dagar för sävsångare. Detta ger en skillnad på 17 dagar mellan de två arterna. När ruggningstiden beräknades utifrån återfångster av tidigare märkta fåglar blev tidsperioderna betydligt kortare, 34 dagar för rörsångare och 22 dagar för sävsångare (Tabell 1). Skillnaden mellan arterna med denna metod blev 12 dagar.

Upplagringen av synligt fett följde i stort sett samma mönster för båda arterna (Fig. 4a och b). Bränsleupplagringshastigheten var ungefär lika hög hos båda arterna, 0,38 g/dag för rörsångare och 0,34 g/dag för sävsångare. Däremot skilde sig arterna åt i mängden lagrat bränsle per fettklass. Rörsångaren lagrade 0,64 g/fettklass medan sävsångaren lagrade 0,30 g/fettklass. Detta innebär att en rörsångare som bedöms som mycket fet (fettklass 6) har en betydligt större bränslereserv (3,49 g) än en sävsångare med till synes lika mycket fett (2,52 g).

Beräkningar av bränslereserverna vid bortflyttning från Kvismaren bygger på data från de 25 % fetaste fåglarna (Alerstam & Lindström 1990) av fåglar i komplett eller så gott som komplett första vinterdräkt (Fig. 5). Enligt denna metod flyttar rörsångarna från Kvismaren med en genomsnittlig bränslereserv på 21 % i förhållande till den fettfria vikten, vilket motsvarar en flygsträcka på 757 km i vindstilla väder (Pennycuick 1989). Sävsångare flyttar däremot i genomsnitt med 6 % bränslereserv vilket motsvarar en flygsträcka på 240 km. Mediandatum för bortflyttningen från Kvismaren beräknades enligt denna metod till 30 augusti för rörsångare och 12 augusti för sävsångare.

Den juvenila ruggningen hos rörsångaren tog 34 dagar beräknat på återfångade fåglar och 48 dagar enligt medianfångstdatum. För sävsångaren var motsvarande tider 22 respektive 31 dagar. De kortare tiderna ligger troligtvis närmare sanningen. Medianfångstdatum skulle kunna påverkas av om individer från nordliga populationer passerar Kvismaren i sena ruggningsstadier och på så vis förlänger fångstperioden (och därmed förskjuter medianfångstdatum) för dessa ruggningsstadier. Att sävsångare ruggade på betydligt kortare tid än rörsångare är dock otvetydigt, oavsett beräkningsmetod.

Ruggningsmönstret skilde sig betydligt åt mellan arterna. Rörsångarens ruggning följde den befintliga skalan, medan sävsångaren sällan bedömdes som intensivt ruggande. En frånvaro av intensiva ruggningsstadier kan bli resultatet om den s.k. ruggningen begränsar sig till en förtätning av fjäderdräkten utan något egentligt fjäderbyte. Müller (1981) har konstaterat att så är fallet för vassångaren *Locustella luscinoides* och det gäller med all sannolikhet även sävsångaren vilken enligt Heinroth & Heinroth (1924–6) föds med en ungfågeldräkt av hög kvalitet och inte byter denna förrän i vinterkvarteren. Detta mönster tycks även gälla för kärrsångare *Acrocephalus palustris*, trastsångare *A. arundinaceus*, vattensångare *A. paludicola*, härmsångare *Hippolais icterina*, polyglottsångare *H. polyglotta* samt de flesta *Locustella*-sångarna (Bensch & Lindström 1992, Cramp 1992).

Bränsleupplagringshastigheten i Kvismaren var för rörsångare hög jämfört med tidigare studier. Gladwin (1963) beräknade den till 0,28 g/dag i England och Bibby & Green (1981) till 0,25 g/dag i Portugal under höstflyttningen. Sävsångaren tycks dock uppnå högre hastigheter vid andra lokaler, upp till 0,58 g/dag i England (Bibby et al. 1976). Det är intressant att mängden lagrat bränsle per fettklass skilde sig så markant mellan arterna. Rörsångaren lagrade nästan lika mycket bränsle per fettklass som en rödhake *Erithacus rubecula*, 0,67–0,85 g/fettklass, medan sävsångaren endast lagrade något mer än en kungsfågel *Regulus regulus*, 0,22–0,25 g/fettklass (Pettersson & Hasselqvist 1985).

De konstaterade olikheterna tyder på att rör- och sävsångaren tillämpar olika flyttningsstrategier, men vid Falsterbo i sydligaste Sverige är skillnaden i bortflyttningsdatum omvänd så att sävsångaren flyttar några dagar *senare* än rörsångaren, dock fortfarande med mindre bränslelager (Falsterbo fågelstation, muntligen). Trots att skillnaderna mellan arterna är uppenbara krävs det ytterligare analyser av data från andra fågelstationer i Sverige och längs flyttningsvägarna i Europa innan några generella slutsatser om orsakerna till och konsekvenserna av detta kan dras.

Meddelande nr 90 från Kvismare fågelstation.