

## Fat accumulation and autumn migration strategy of Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *A. schoenobaenus* in southern Sweden

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In order to investigate fat accumulation and the migration strategy of Reed and Sedge Warblers during autumn, their pattern of fat deposition at the onset of migration was recorded and analysed using ringing data from three bird observatories, at Kvismaren, Getterön and Falsterbo in southern Sweden. The data suggest that the birds have adopted a strategy where they do not use all accumulated fat during a single migratory flight, but travel with a higher fat load than necessary for the specific flight stage. By arriving at the next stopover site with some fat remaining, the birds become less vulnerable to the quality of stopover sites and variation in food availability during migration.

Migratory birds use fat as their main source of energy and, to migrate long distances, need to accumulate large amounts of fat before migration and during feeding at stopover sites en route. It is thus crucial that the food is sufficiently abundant at stopover sites, particularly at sites where a large proportion of a population may pass through. Extensive feeding is costly, both with respect to energy expenditure and exposure to predators, although the true significance of mortality in this respect has been questioned (Dierschke 2003).

Within optimal bird migration theory (Alerstam & Lindström 1990), three major factors contribute to the migration strategy of a bird, time constraints, energy economy and predation risk. As a large amount of body fat may hamper escape from a predator (eg Kullberg *et al* 1996, 2000), birds at high risk from predation pressure are thought to accumulate less fat than those migrating under time constraints (predation-selected migration of Alerstam & Lindström 1990). The lower amount of fat will take a bird to the next suitable feeding site, but not much farther, although it is likely that many birds keep a safety margin of fat for the time between arrival at a stopover site and the actual start of feeding (settling time of Alerstam & Lindström 1990). The predation-selected migration strategy has the advantages that the birds keep a higher level of mobility and also use more of the stored energy for migration, as large fat deposits also demand more energy for birds to move.

For the strategy to function well, easily found and relatively closely spaced stopover sites, with high abundance of food, are important. As food availability

in future stopover sites is difficult to assess, it could prove advantageous to accumulate more fat than necessary to reach the next site and thus increase fat load stepwise (Schaub & Jenni 2001). In contrast, birds that can expect long distances between favourable stopover sites will always accumulate high fat loads as they have to travel long distances without eating. The latter strategy is evolutionarily necessary only for crossing ecological barriers, such as deserts and oceans (Alerstam & Lindström 1990, Weber & Houston 1997, Alerstam & Hedenström 1998, Hilgerloh & Wilschko 2000).

Sedge Warbler *Acrocephalus schoenobaenus* and Reed Warbler *A. scirpaceus* are small warblers of roughly the same size, inhabiting similar, but not entirely identical habitats. Sedge Warblers prefer areas at the edge of the reed beds, habitats with bushes and tall herbage, whereas Reed Warblers are more strongly associated with extensive reed beds during breeding. The distinction is not absolute, however, and each species may breed in areas usually considered more favourable for the other. European Sedge Warblers spend the winter in areas south of the Sahara, but seem to be widespread over larger parts of sub-Saharan Africa, whereas most Reed Warblers (of the nominate subspecies) apparently prefer the western parts of the continent (eg Fransson & Stolt 2005, Procházka *et al* 2008). These birds usually choose a southwesterly route through Europe and cross the Mediterranean from the Iberian Peninsula (Fransson & Stolt 2005, Fransson & Hall-Karlsson 2008). In contrast, Sedge Warblers breeding in Sweden head south or southwest after breeding and the majority appear to cross the Mediterranean over Italy (Fransson & Hall-Karlsson 2008). Reed Warblers feed largely on active insects,

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especially dipterans, and feed often in bushes, which is why the birds are not particularly dependent on wetlands during migration. It was previously believed that Sedge Warblers are especially adapted to feeding on non-flying insects (Bibby *et al* 1976, Bibby & Green 1981), but more recent investigations conclusively show that these birds feed on a wide variety of insects and other arthropods (Chernetsov & Manukyan 2000). Their need for wetlands as stopover sites may thus be exaggerated but is difficult to assess at present.

The aim of this study was to investigate fat accumulation behaviour at the onset of autumn migration in Reed and Sedge Warblers in southern Sweden and analyse migration strategy in the Swedish population of the two species, based on fat accumulation patterns. Previous studies have investigated fat accumulation in general terms, but a better understanding of fat accumulation strategies may be obtained by comparisons between sites at the initial stages of migration.

## METHODS

### Study sites

#### Kvismaren

Lake Kvismaren consists of two shallow, eutrophic lakes that have been restored and is situated in central southern Sweden (59.10°N 15.25°E). Ringing is conducted there on a daily basis between the end of June and end of September at three sites on a rotating schedule. The sites are less than 10 km apart, two of them located at Lake Kvismaren and one on the south end of the island of Ässön in Lake Hjälmaren. Large numbers of Sedge and Reed Warblers breed at Lake Kvismaren and ring recoveries show that additional migrating birds of both species forage in the area during late summer and autumn. The site at Ässön has a higher proportion of migrating birds than the sites in Lake Kvismaren. Post-juvenile moult has been recorded since 1984 and data used in this study therefore derives from 1984–2009. A total of 13,959 Sedge Warblers and 13,881 Reed Warblers have been included in the study (Table 1).

#### Getterön

Getterön is a coastal bay with a small area of reed beds situated on the west coast of Sweden (57.08°N 12.15°E). Ringing is conducted from mid July till the end of October. Only a small number of Reed and Sedge Warblers breed within the area but ring recoveries indicate that migrating Reed Warblers from central Sweden stop over at Getterön. Sedge Warblers are not

**Table 1.** Number of birds included in the analysis from the three ringing sites.

		Kvismaren	Getterön	Falsterbo
Reed Warbler	Adult	5,663	858	11,025
	First-year	8,218	2,211	20,147
Sedge Warbler	Adult	1,845	139	1,613
	First-year	12,114	341	10,318

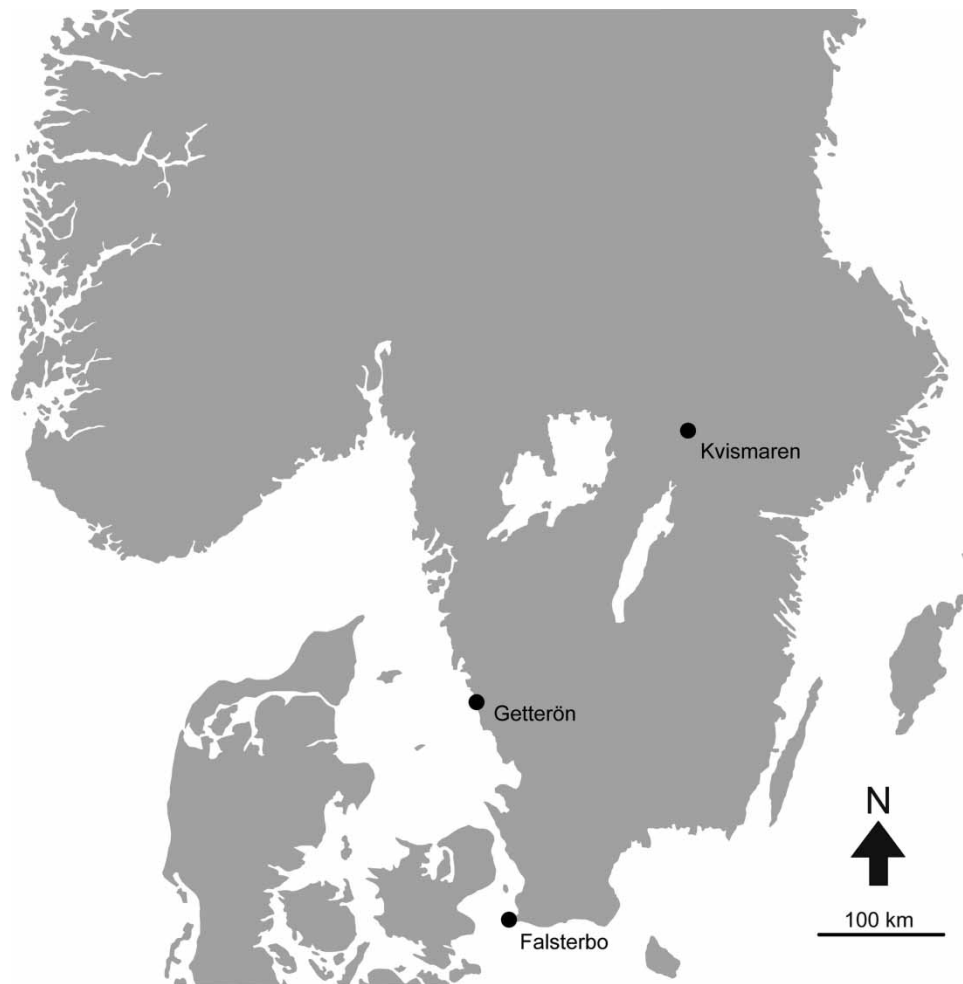
ringed in large numbers at this site and are strongly outnumbered by Reed Warblers. At Getterön, the post-juvenile moult scale has been in use since 1998 and the number of birds included in this study was 480 Sedge Warblers and 3,069 Reed Warblers (Table 1).

#### Falsterbo

Falsterbo is situated on the southwesternmost peninsula of Sweden (55.24°N 12.50°E). Ringing takes place at two different sites but Reed and Sedge Warblers are ringed primarily at Flommen, an area of coastal lagoons with small reed beds. Ringing is conducted from 15 July until 30 September. Apart from a small number of breeding birds, the overwhelming majority of birds ringed are on migration at the site. The post-juvenile moult scale has been in use since 1986, with 11,931 Sedge Warblers and 31,172 Reed Warblers included in this study (Table 1).

## Data

The two warbler species studied have different moult strategies. Adult and juvenile Reed Warblers conduct a partial moult of body-feathers before migration. Adult Sedge Warblers do not moult prior to autumn migration, whereas only a proportion of juvenile Sedge Warblers will have a partial moult of some body-feathers and the extent of geographical variation has not been established (Svensson 1992, Redfern & Alker 1996). Separating adult birds from juveniles or first-years of the two species is rarely problematic and we have followed Svensson (1992 and earlier editions) in our material. For our analyses, we used ringing data including new birds and recaptures, and in particular fat score and post-juvenile moult score, from bird observatories at Kvismaren, Getterön and Falsterbo (Fig 1). All these bird observatories use mist nets and standardised methods to capture birds. In order to study only birds in the process of migration, we included fat-storage data for yearlings in post-juvenile moult stages 5 or 6 only (Bensch & Lindström 1992), as those in stages 1–4 are



**Figure 1.** Southern Scandinavia and the location of the ringing sites in Sweden.

unlikely to travel long distances (Boddy 1983, Norman 1991), and additionally show low fat scores. All adult birds were included in the material.

The amount of visible fat beneath the skin of the abdomen of the birds was classified on a ten-point scale from 0 (no visible fat) to 9 (entire abdomen covered by fat), a scale introduced by Pettersson & Hasselquist (1985) and later modified by Falsterbo Bird Observatory (unpublished). The modifications mainly include three added categories describing high fat levels, with visible fat extending onto the breast. Compared to the European Science Foundation (ESF) scale (Kaiser 1993), the Falsterbo scale has an extra category between ESF 0 and 1, so that Falsterbo level 2 roughly corresponds to ESF level 1 and Falsterbo level 9 corresponds to ESF level 8. The fat scale used in this investigation provides a detailed determination of the fat load of an

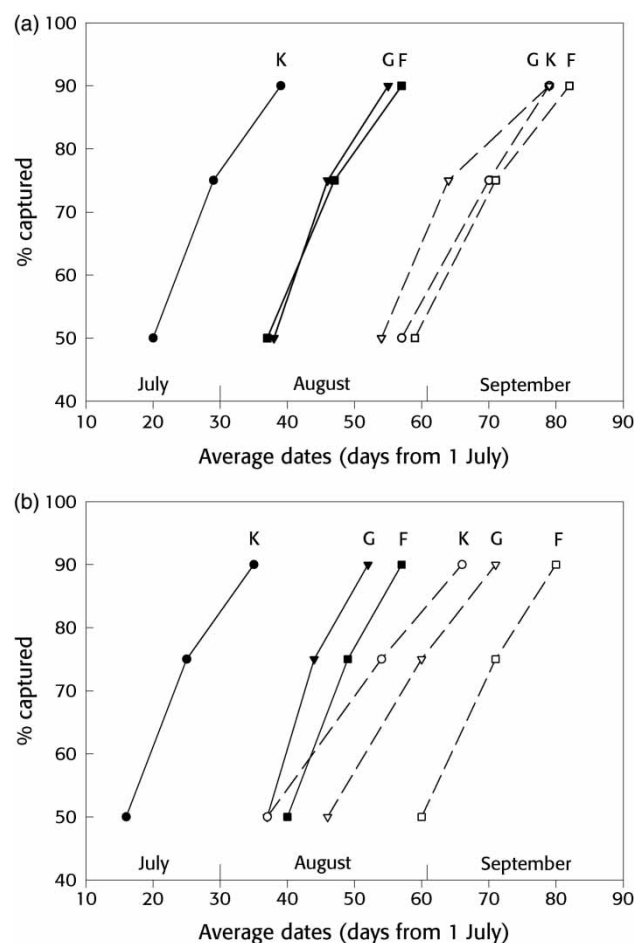
individual bird and is independent of body size and capture time. It is a non-linear scale but nevertheless serves the purpose of this study well, as migratory birds can be separated from those not yet in the process of migration. The birds increase in fat load until they depart, which leads to the recorded mean fat load in the population at any given moment being a minimum level. It has also been shown that birds with a high amount of fat are less frequently captured in mist nets, probably because they are more reluctant to fly (eg Bibby *et al* 1976). We have refrained from using body mass as this measure depends on other factors than fat alone and because the study has been carried out during a long period of time and different kinds of scales have been used. For the statistical analysis, we used regression models using SPSS statistics v17.0.

### Theoretical assumptions

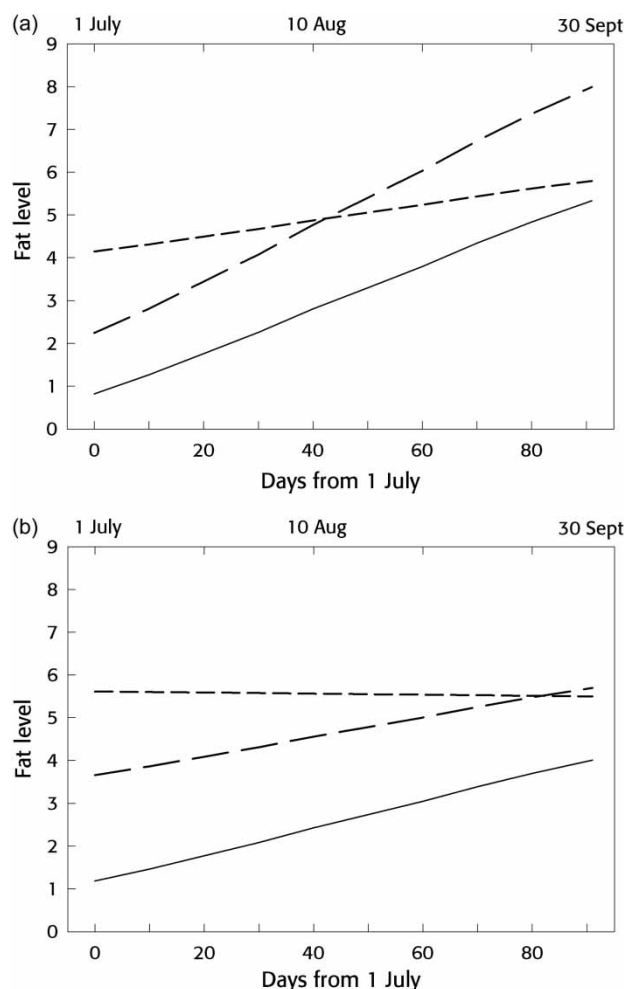
During the migratory season, any given population of birds at a specific site consists of birds that have not yet started their fat accumulation, birds in different stages of pre-migratory fat accumulation and birds that are ready to migrate. In the last two groups, there may be resident birds as well as birds in stopover after one or more migration stages. The mean fat-accumulation levels of ringed birds in a certain period can be assumed to be dependent on the proportion of birds that are in different stages of fat accumulation, the proportion of birds that has not yet started to accumulate fat and finally the amount of fat that is accumulated before migration. The mean fat load

should increase during the migratory season as the proportion of birds actively accumulating fat increases, even though a larger proportion of birds also migrate.

If two sites have the same composition of birds in different stages of fat accumulation, then the average fat load at any given time during the season should be equal. It can be hypothesised that if the increase over time is equal but the level of fat differs between sites, this would suggest different fat loads at time of departure. In contrast, different increases over time suggests that the composition of birds is unequal.



**Figure 2.** Temporal distribution of migrating Reed Warblers (a) and Sedge Warblers (b) at the Kvismaren (K; circles), Getterön (G; triangles) and Falsterbo (F; squares) sites as indicated by average dates when 50%, 75% and 90% of the birds had been captured. Solid lines and filled symbols represent adults, and dashed lines with open symbols first-year birds.

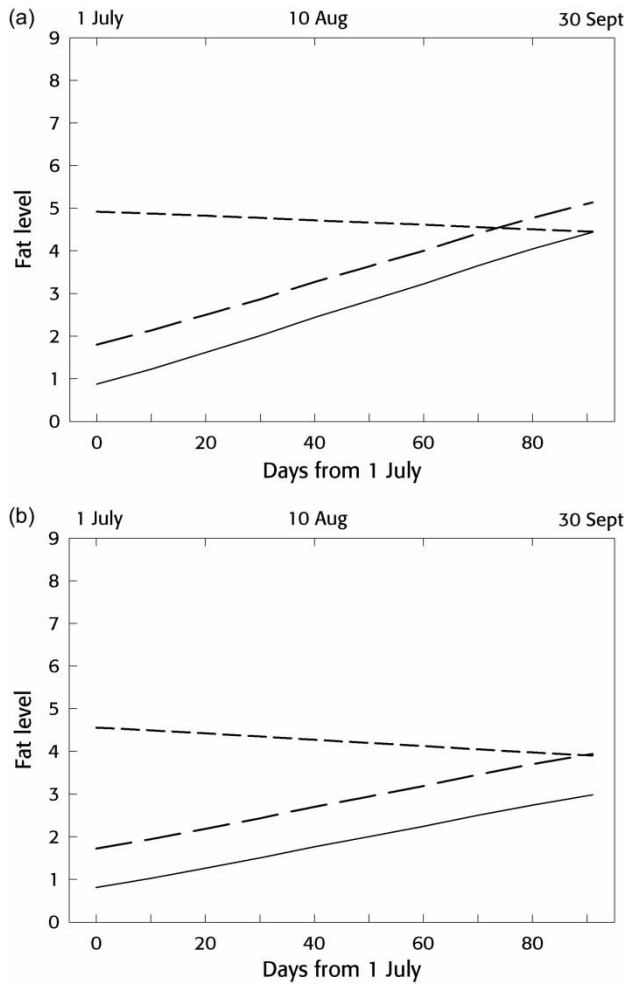


**Figure 3.** Predicted fat load for (a) adult and (b) first-year Reed Warblers. Solid line is for Kvismaren, long-dashed line is for Getterön and short-dashed line is for Falsterbo.

RESULTS

The timing of migration from Kvismaren differs between the two species as well as between age groups (Hall 1996) of both species. The adults leave the area before the first-year birds of both species, and Sedge Warblers migrate earlier than Reed Warblers (Fig 2). Reed Warblers and Sedge Warblers had similar arrival times at Falsterbo but Sedge Warblers were earlier at Kvismaren and later at Getterön. At Kvismaren and Getterön, mean fat load increased during the migratory season for both species and age groups, whereas at Falsterbo, it was only adult Reed Warblers that showed signs of fat load increase during the season (Figs 3 & 4).

We analysed the predicted mean fat load by a regression analysis with all sites (Table 2). Our analysis also compares



**Figure 4.** Predicted fat load for (a) adult and (b) first-year Sedge Warblers. Solid line is for Kvismaren, long-dashed line is for Getterön and short-dashed line is for Falsterbo.

**Table 2.** Regression analyses of fat-load development during the season.

	Coefficient	t†	P†
<i>Reed Warbler first-year</i>			
Constant	2.08	218.05	<0.001
Date	0.03	52.87	<0.001
Getterön	2.68	70.87	<0.001
Falsterbo	3.47	207.82	<0.001
Interaction between Date and Getterön	-0.00	-1.85	>0.06
Interaction between Date and Falsterbo	-0.28	-30.39	<0.001
<i>Reed Warbler adult</i>			
Constant	2.75	70.22	<0.001
Date	0.05	29.12	<0.001
Getterön	1.95	28.26	<0.001
Falsterbo	2.10	49.75	<0.001
Interaction between Date and Getterön	0.01	-2.95	<0.05
Interaction between Date and Falsterbo	-0.32	-14.89	<0.001
<i>Sedge Warbler first-year</i>			
Constant	1.67	138.79	<0.001
Date	0.01	23.54	<0.001
Getterön	1.10	13.70	<0.001
Falsterbo	2.23	101.55	<0.001
Interaction between Date and Getterön	0.20	2.31	<0.05
Interaction between Date and Falsterbo	0.21	2.48	<0.05
<i>Sedge Warbler adult</i>			
Constant	2.40	35.89	<0.001
Date	0.04	5.99	<0.001
Getterön	0.83	30.91	<0.001
Falsterbo	2.32	-0.25	>0.80
Interaction between Date and Getterön	-0.00	2.31	<0.05
Interaction between Date and Falsterbo	-0.00	-11.22	<0.001

† t and P refer to test of coefficients being equal to zero.

explained and unexplained sum of squares, standard error and F-value for three different models, one with the assumption that intercept and slope are equal between sites, one where intercept may differ while slope is constant, and finally the chosen model where both intercept and slope may differ between sites (Table 3). The results show that for first-year birds and adults of



**Table 3.** Stepwise ANOVA table for three models, one with the assumption that intercept and slope are equal between sites (Date), one where intercept may differ while slope is constant (Date and Site), and finally, the chosen model where both intercept and slope may differ between sites (full model with interaction between Site and Date).

	Sum of squares	Residual sum of squares	df	F	r <sup>2</sup>	SE	P
<i>Reed Warbler first-year</i>							
Date	38,255	240,247	1	7,945	0.14	2.19	<0.001
Date and Site	152,525	125,976	3	20,136	0.55	1.59	<0.001
Full model with interaction between Site and Date	154,824	123,678	5	12,491	0.56	1.57	<0.001
<i>Reed Warbler adult</i>							
Date	21,869	64,089	1	5,986	0.25	1.91	<0.001
Date and Site	37,656	48,302	3	4,559	0.44	1.66	<0.001
Full model with interaction between Site and Date	38,420	47,538	5	2,835	0.45	1.65	<0.001
<i>Sedge Warbler first-year</i>							
Date	17,410	78,053	1	5,790	0.18	1.73	<0.001
Date and Site	39,632	55,831	3	6,142	0.42	1.47	<0.001
Full model with interaction between Site and Date	39,694	55,768	5	3,695	0.42	1.47	<0.001
<i>Sedge Warbler adult</i>							
Date	5,600	10,198	1	1,974	0.35	1.68	<0.001
Date and Site	8,936	6,862	3	1,560	0.57	1.38	<0.001
Full model with interaction between Site and Date	9,174	6,624	5	995	0.58	1.36	<0.001

both species, there was significantly higher mean fat levels at Getterön than at Kvismaren and the fat load was even higher at Falsterbo than at Getterön for both species and age groups except for adult Reed Warblers. The slope of the regression was not significantly different at Getterön compared to Kvismaren but at Falsterbo the slope was significantly less steep, with the exception of adult Reed Warblers (Table 2, Figs 3 & 4). At the end of the migratory season, when 90% of the birds had been ringed at Kvismaren, the mean fat scores of first-year Reed Warblers were >1.5 levels higher at Getterön and Falsterbo than at Kvismaren (Fig 3). The fat load of adult Reed Warblers was >2 levels higher at Getterön but <2 levels higher at Falsterbo, compared to Kvismaren (Fig 3). First-year Sedge Warblers had slightly less than one level higher fat load at Getterön than at Kvismaren, and at Falsterbo, the difference from Kvismaren was 1.5 levels (Fig 4). Finally, adult Sedge Warblers had greater fat load (by 0.8 of a level) at Getterön and nearly two levels higher at Falsterbo than at Kvismaren, when 90% of the birds had been ringed (Fig 4).

## DISCUSSION

### Fat accumulation in Sweden

The material from Kvismaren and Getterön appears to include similar proportions of birds in different fat

loading stages throughout the season, as shown by roughly parallel regression lines in Figs 3 & 4. At Falsterbo, on the other hand, all birds seem ready to migrate, as shown by more-or-less horizontal regression lines. Collectively, these data imply that there is an increasing fat load within Sweden during the early stages of the migration and that both Reed and Sedge Warblers leave Sweden with high fat loads.

According to the widely accepted concept of optimal bird migration (Alerstam & Lindström 1990), the high fat loads, reaching up to 50% of the lean weight in many birds at Kvismaren (unpublished data), suggest that the birds travel long distances after leaving the ringing sites. As inferred from ring recoveries (Fransson & Hall-Karlsson 2008), the next stop for the Sedge Warblers would be an area encompassing northern Italy, Slovenia and Croatia, suggesting either that there would be few suitable feeding areas in central Europe on the autumn migration for the species or that the birds are under time constraints. In the case of the Reed Warbler, the high fat loads may suggest non-stop flights to the Iberian Peninsula (Fransson & Hall-Karlsson 2008), where the birds would feed before crossing the Sahara Desert, as Reed Warblers from Britain do (Bibby & Green 1981).

An alternative and perhaps more reasonable model is that both Sedge and Reed Warblers adopt a different

strategy, where the lowest fat load increases in each short migration step, *ie* a staircase strategy where some fat is used and then foraging increases the fat load progressively to a higher level than at the previous stopover. The fact that the birds move through Sweden with increasing fat loads and leave the country with high loads, despite not encountering any ecological barriers, supports this model. However, there are ring recoveries, though few in number, which indicate that Sedge and Reed Warblers may migrate for up to three consecutive nights before refuelling (Hall-Karlsson & Fransson 2008). By doing so, they would fly across benign areas suitable for foraging but, instead of refuelling often, increase their migratory speed. Another advantage of accumulating high fat loads stepwise would be that the birds are less vulnerable to variations in food availability across Europe, a factor that is difficult for the birds to predict (Schaub & Jenni 2001). They will also arrive at their final accumulation site before crossing the Mediterranean and the Sahara without having to amass a full fat load. Adult Sedge Warblers arriving in northern Italy display moderate levels of fat whereas the first-year birds show a distinctly lower level (Basciutti *et al* 1997), perhaps indicating that the more experienced adults are more successful in their adaptation to the strategy or better at locating food during short stopovers. The disadvantages of the suggested strategy include being more vulnerable to predators, as birds with high fat loads are less mobile, as was shown specifically for the Sedge Warbler by Kullberg *et al* (2000). Another disadvantage that could be argued is that it is more expensive to fly with a high fuel load, but it appears less so than expected, at least for waders (Kvist *et al* 2001), and if transferrable to warblers may actually strengthen the theory and lead to higher migration speed. The suggested strategy is easier to explain in evolutionary terms when it comes to making an appropriate fat accumulation at a particular site and more advantageous than to use all stored fat between stopover sites. A similar strategy, albeit on a smaller scale, appears to be adapted by spring migrating warblers of both species, where many birds arriving in the morning had enough energy to allow them to continue migrating for at least another night (Bolshakov *et al* 2003a, b). Naturally, spring migration requires a separate strategy as time constraints are more stringent for birds trying to reach their breeding grounds as soon as possible, but the strategy may allow the birds to arrive on their territories with a positive energy balance.

In conclusion, both Reed Warblers and Sedge Warblers depart on their autumn migration with high fat loads from southern central Sweden, but despite this, there is

further accumulation of fat in the early stages of the migration within Sweden. The adaptive nature of this strategy can be explained either by regarding central Europe as an ecological barrier with few fuelling possibilities and high competition at the available fuelling sites, or by assuming that the birds employ a migratory strategy in which they do not use most of the stored fuel during each migratory stage.

### Aspects of migratory routes

As parts of the large British Sedge Warbler population appear to migrate to northwestern France in order to forage on reed aphids in the relatively few suitable areas available (Bibby & Green 1981), the competition is likely to be high in these areas even if the birds are not as dependent on high abundance of reed aphids as previously thought (Chernetsov & Manukyan 2000). Few Sedge Warblers ringed in Britain have been recovered in the Iberian Peninsula, indicating that these birds travel directly from northern France to North Africa (Wernham *et al* 2002). Ring recoveries have shown that the Sedge Warblers breeding in Sweden migrate over the central parts of the Mediterranean and it is likely that they stop over in Italy (at rice paddies), Slovenia and Croatia and perform a final accumulation of fat before migrating across the Mediterranean and the Sahara (Fransson & Hall-Karlsson 2008). Sedge Warblers of Scandinavian origin have been recorded stopping over in northern Italy with low to moderate fuel levels and leave study areas without refuelling, indicating that there may be more favourable localities further south (Basciutti *et al* 1997). Suitable localities with high abundance of food may be restricted, forcing the birds to migrate stepwise between these sites.

Several studies have concluded that Reed Warblers feed largely on active insects, mainly dipterans, and consequently they can feed in bushes and shrubs without being dependent on wetlands as stopover sites (Bibby *et al* 1976, Davies & Green 1976). Intraspecific competition could possibly be lower than in the Sedge Warbler as Reed Warblers appear more generalistic in both feeding technique and the range of environments in which they stop over. Ring recoveries show that the Swedish population migrates through western Europe to the Iberian Peninsula before the final accumulation of fat needed for the trans-Saharan migration. The birds of any given population may migrate slowly through Europe and use many different stopover sites (Bibby *et al* 1976). The large numbers of recoveries in Belgium of Reed Warblers ringed in Sweden may be regarded as an indication of migratory routes, but not of stopover

sites as the birds are lured to the ground by playback of their song (see Schaub *et al* 1999).

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