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Fat-weight relationships and migratory strategies in the Robin *Erithacus rubecula* at two stop-over sites in south Sweden

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Robins captured during spring and autumn migration 1986 at Falsterbo and Ottenby, south Sweden were compared as to fat deposition, body weight and size (measured as wing length). Though the birds from the two sites were of practically the same size, significant differences in fat deposition and body weight were found. The Robins captured at Falsterbo were heavier but carried less fat than the Ottenby Robins. The differences were more obvious in the lower fat classes in autumn birds, more constant through all fat classes in spring birds.

These results indicate that Robins from the two sites use different migration strategies. Probably, many Falsterbo Robins are "short-stage migrants", travelling over land, and needing only small fat reserves, while the Ottenby Robins are "long-stage migrants" needing large fat reserves to complete their flight across the Baltic Sea. This pattern fits in well with other studies on Robins from the two sites (reports of ringed birds, orientation experiments). We also speculate that the differences in body weight may reflect different water contents. The Falsterbo Robins may have a high water content and/or the Ottenby Robins may be dehydrated. Seasonal variation in fat-weight relationships support the suggested patterns.

The results also show that the amount of fat in migrating Robins cannot be estimated reliably on the basis of weight data alone.

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INTRODUCTION

The Robin *Erithacus rubecula* has been the subject of extensive studies based on ringing data. The migration of the Fennoscandian Robins has been analysed from different points of view by, among others, Rendahl (1966), Högstedt & Persson (1971), Pettersson 1983 a,b), Pettersson & Lindholm (1983), Saurola (1983), Roos (1984) and Pettersson & Hasselquist (1985).

Fat deposition and body weight are two components often used in analyses of migration strategies, since they make it possible to estimate the theoretical flight range for migrating birds (Odum et al. 1961, Nisbet et al. 1963, Pennycuick 1975, Hussel & Lambert 1980, Davidson 1984, Pettersson & Hasselquist 1985). Besides fat, other components like water content and protein reserves may have important effects on body weight (Helms & Smythe 1969, Moreau & Dolp 1970, Fogden 1972, Baggott 1975, Davidson 1986 a,b).

This paper presents data on fat deposition and body weight in Robins captured, during autumn and spring migration, at Falsterbo Bird Observatory (55°23'N, 12°49'E) on the southwestern point of Sweden, and Ottenby Bird Observatory (56°12'N, 16°24'E) on the south point of Öland, SE Sweden (see Fig. 4). The differences in fat-weight relationships between sites, seasons and age groups are evaluated and discussed, in relation to recovery patterns of ringed birds, and to recent orientation experiments on Robins from the two sites (Sandberg et al. 1988).

MATERIALS AND METHODS

Robins captured at Falsterbo and Ottenby during the spring and autumn migrations in 1986 were used for analyses in this paper. At Falsterbo Bird Observatory, the birds were trapped in mist-nets set in the Lighthouse garden, during the standardized ringing scheme, which operates from 21 March to 10 June and from 21 July to 10 November. The Robins at Ottenby Bird Observatory were trapped in mist-nets or Heligoland traps also during the standardized ringing scheme which operates from 15 March to 15 November. Thus the complete spring and autumn migration periods of Robins were well covered at both sites.

The birds were aged according to Pettersson (1983 c) and Karlsson et al. (1986), using the presence of unmoulted juvenile greater coverts as first criterion in juveniles (Euring code 3 in autumn, 5 in spring). We use the term "juvenile" here as a shorthand label for birds up to their first complete moult at the age of one year. The ageing method is based on the colour contrast between inner moulted and outer unmoulted greater coverts, the latter being more brownish, and also often having larger yellowish spots at tips. In a sample of more than 3000 juveniles, 95% had 4-7 unmoulted greater coverts and none had moulted all (Karlsson et al. 1986). The method provides a far better age separation than the upper mandible method described by Svensson (1984), especially in spring.

Wing length was measured to the nearest 1 mm, according to Method 3 (maximum chord) in Svenssson (1984). Fat deposits were estimated visually, following the classification made by Busse & Kania (1970), with an additional class as shown by Pettersson & Hasselquist (1985). The birds were weighed to the nearest 0.1 g with a 50 g Pesola spring balance.

We are confident that both the wing length measurements and the fat class determination were made equally at both sites. The supports for this statement are: (A) Calibration and tests of measuring have been made between the authors. Test results are shown in Table 1. (B) All measurements were collected by the authors or after careful instruction and supervision by them. (C) The fat class differences for a specific weight are so large, that they can hardly be a consequence of unequal classification (cf. Figs. 2 and 3). (D) The largest weight differences are in fat class 0 (no fat), which is the easiest to identify. (E) Fat-weight relationships from Algutsrum (see Fig. 1) are similar to those from Falsterbo, but differ from those from Ottenby, although the determinations at Algutsrum and Ottenby were made or supervised by the same person (JP).

RESULTS

Data on fat class distribution, body weight and wing length are presented in Table 2 for Robins from the two capture sites, separately for spring and autumn migrants, and for adults and juveniles. In Table 3 the statistical significance levels for differences in fat class distribution, mean body weight and mean wing length are shown. Adults have more fat than juveniles, in spring as well as in autumn, both at Falsterbo and Ottenby. Juveniles have more fat in spring

TABLE 1. Test of fat class determination and measuring of wing length between observers from Falsterbo (G. Walinder) and Ottenby (J. Pettersson).

Fat class determination (N =82)

OTTENBY \ FALSTERBO	*0*	*1*	*2*	*3*	*4*	*5*	*6*
0	6						
1		5					
2			8				
3				10	2		
4				1	19		
5					1	24	1
6						4	

Wing length (N =50)

OTTENBY \ FALSTERBO	*69*	*70*	*71*	*72*	*73*	*74*
69	3					
70		5				
71		1	13	2		
72				12		
73				1	9	1
74						3

TABLE 2. Robins captured at Falsterbo and Ottenby Bird Observatories 1986 divided into seasons and age classes. For each category, sample size, fat class distribution, mean fat class, mean body weight (±SD) and mean wing length (± SD) are shown.

Site	Season	Age	N	Fat class 0	1	2	3	4	5	6	x	Mean weight	SD	Mean wing length	SD
FALSTERBO	Autumn	Ad	130	5	14	25	41	33	12	0	2,92	16,34	0.95	73,82	1,99
		Juv	996	141	250	279	203	90	30	3	1,95	15,84	0,94	73,23	1,81
	Spring	Ad	177	5	22	34	55	41	18	2	2,94	16,32	1,08	73,50	1,91
		Juv	421	24	79	115	107	65	29	2	2,49	15,92	1,18	72,67	1,88
OTTENBY	Autumn	Ad	126	3	11	19	26	33	30	4	3,44	15,73	1,93	73,41	2,13
		Juv	1071	27	127	214	340	189	165	9	3,00	15,26	1,89	72,98	2,08
	Spring	Ad	172	0	8	26	41	49	47	1	3,61	15,56	1,42	73,27	1,94
		Juv	1182	6	69	214	425	301	162	5	3.23	15,21	1,80	72,77	1.75

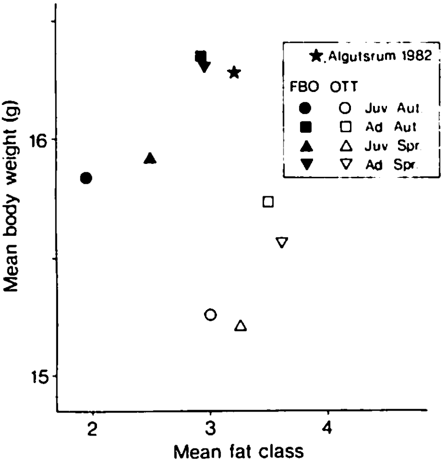

FIGURE 1. The relationship between mean body weight and mean fat class in Robins captured at Falsterbo (filled signs) and Ottenby (open signs) during spring and autumn migration 1986. Sample sizes are shown in Table 1. Data from Algutsrum 1982 (n = 121) refer to birds in a premigratory fat-accumulating status captured at a woodland site in autumn (from Pettersson & Hasselquist (1985), cf. text).

than in autumn, while adults show no such differences between seasons.

We assume that the mean wing length within the same age group is proportional to the average body size of the birds. However, the difference in mean wing length between age groups does not necessary reflect any important difference in body size, but may rather be related to the fact that after their first complete moult, birds get somewhat longer wings (Stewart 1963, Alatalo et al. 1984). Also, wing tips of juveniles will abrade more during the winter. In juveniles, there is a difference in mean wing length between seasons, especially at Falsterbo. This is probably due to a larger proportion of females, having shorter wings than males, in spring captures (Mehlum 1981, Pettersson & Lindholm 1983), rather than abrasion of wing tips.

Comparisons of birds from the two sites, show that there are significant differences in fat class distribution and mean body weight, but not in mean wing length (Table 3). The difference in mean wing length is less than 1%, only significant in one single case (juveniles in autumn), indicating that there are no consistent differences in body size between the Robins captured at Falsterbo and Ottenby.

Robins at Falsterbo have less fat than Robins at Ottenby, but, in spite of this, the Falsterbo Robins are distinctly heavier than the Ottenby birds (Table 2 and Fig. 1). This indicates that components other than fat can affect the body weight to a considerable extent.

The relationships between body weight and visually estimated fat class are shown for Robins captured at Falsterbo (Fig. 2A) and

TABLE 3. Significance levels for differences in fat class distribution (Kolmogorov-Smirnov two-tailed test), mean body weight (two-tailed t-test) and mean wing length (two-tailed t-test) in Robins captured at Falsterbo and Ottenby. Samples shown in Table 1. (n.s. = not significant, $p>0.05$).

		Fat class distribution	*Mean body weight*	*Mean wing length*
Falsterbo				
Autumn	Juv / Ad	0.001	0.001	0.001
Spring	Juv / Ad	0.005	0.001	0.001
Juv	Autumn / Spring	0.001	n.s.	0.001
Ad	Autumn / Spring	n.s.	n.s.	n.s.
Ottenby				
Autumn	Juv / Ad	0.001	0.01	0.05
Spring	Juv / Ad	0.001	0.02	0.001
Juv	Autumn / Spring	0.001	n.s.	0.01
Ad	Autumn / Spring	n.s.	n.s.	n.s.
Autumn				
Juv	Fbo / Ott	0.001	0.001	0.01
Ad	Fbo / Ott	0.025	0.01	n.s.
Spring				
Juv	Fbo / Ott	0.001	0.001	n.s.
Ad	Fbo / Ott	0.001	0.001	n.s.

Ottenby (Fig. 2B). There is little variation at either site in mean body weight between adults and juveniles and between autumn and spring birds for any given fat class. Hence, at each site the different categories of Robins show virtually the same fat-weight relationships. The only notable differences were found in juveniles; in some (Falsterbo) or most (Ottenby) of the fat classes they were significantly heavier in autumn than in

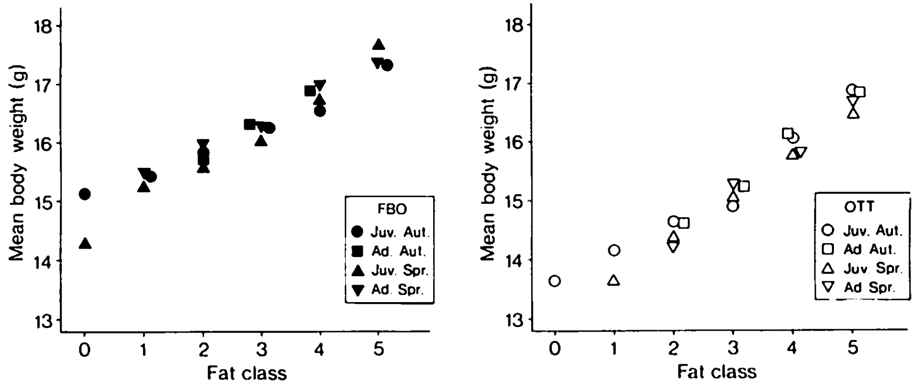

FIGURE 2. Fat-weight relationship in Robins captured at Falsterbo (A) and Ottenby (B) divided into seasons and age groups. Sample sizes are shown in Table 1. Sample <15 are excluded in Fig. Standard deviations are not possible to show in Fig. but complete data will be sent on request.

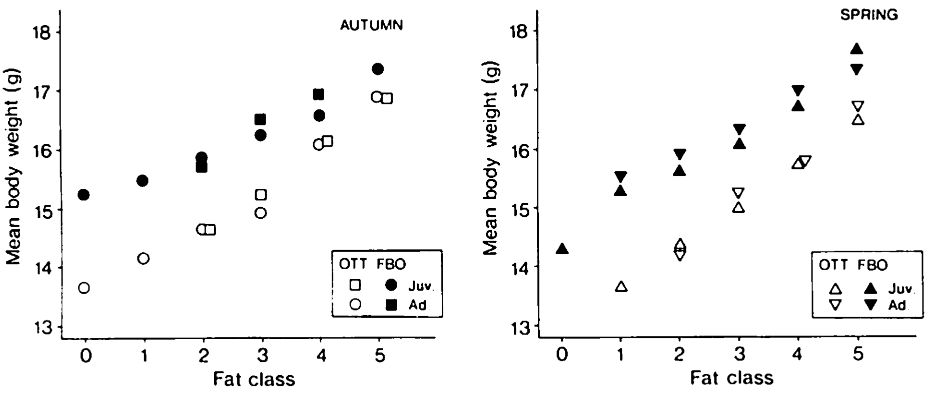

FIGURE 3. Fat-weight relationship in Robins captured in autumn (A) and spring (B) at Falsterbo (filled signs) and Ottenby (open signs). Sample sizes are shown in Table 1. Samples <15 are excluded in Fig. Standard deviations are not possible to show in Fig. but complete data will be sent on request.

spring (t-test: FBO: Fat class 0 $p<0.001$, fat class 2 $p<0.05$. OTT: Fat class 1 $p<0.001$, fat classes 2,4,5 $p<0.01$).

In contrast to the relatively small differences in fat-weight relationships between categories of migrants at each site, there are conspicuous differences between birds from the two capture sites. Comparisons are shown in Fig. 3 for autumn (3A) and spring (3B) birds respectively. For each fat class, age group and season, the Falsterbo Robins are significantly heavier (t-test, $p<0.001$) than their conspecifics at Ottenby.

In autumn, the greatest differences are in the lower fat classes. Juveniles in fat class 0 at Falsterbo are on average 1.5 g heavier than the corresponding category at Ottenby, whilst in fat class 1 the difference is 1.3 g. The mean weight gain per fat class is 0.44 g for the Falsterbo Robins and 0.64 g for the Ottenby birds. Thus the difference in body weight decreases in the higher fat classes, and is only 0.5 g in fat class 5.

In spring, the mean weight difference between juveniles from the two sites is 1.6 g in fat class 1 and 1.2 g in fat class 5. The mean weight gain per fat class is 0.67 g for the Falsterbo Robins and 0.71 g for the Ottenby birds, so that the differences are more constant through fat classes than in autumn.

Why do these different fat-weight relationships occur? As shown in Table 1, errors caused by the method of estimating fat deposits can be excluded. Also, there is no significant difference in wing length between birds of the same age group from the two capture sites. Hence, since we accept wing length as proportional to body size, the Robins at Falsterbo and Ottenby are of the same average body size and this factor provides no clue to the observed differences in fat and weight.

Fat deposition

The fat class distribution (Table 2) shows that Robins from Falsterbo are on average less fat than the Robins captured at Ottenby. The difference is more obvious in autumn than in spring, and is greater in juveniles than in adults. We suggest that these differences are associated with two distinct migration strategies; one used by the Robins captured at Falsterbo, and the other used by Robins caught at Ottenby.

In autumn, most Robins arrive at Falsterbo after migration over land in southern Sweden, while those arriving at Ottenby have usually completed a long-distance flight across the Baltic Sea. The Robins captured at Ottenby carry enough fat to continue their journey across the sea without refuelling (Pettersson & Hasselquist 1985). Thus, the birds are well adapted to long-distance flights. At Falsterbo, the Robins carry much less fat (but are heavier), indicating a short step migration strategy. As shown by Norman (1987), only modest levels of fat are necessary for short distance migratory flights. Perhaps also some other kind of fuel (glucose?) is sufficient for these short flights, especially since so many birds were in fat class 0. When arriving at the south coast of Sweden and at Falsterbo, the Robins hit a migration barrier, the Baltic Sea. Some fat accumulation may be necessary, before the birds make a sea-crossing, so that they may return inland in search of suitable resting areas (see Alerstam 1978 for a discussion of this strategy). Similar behaviour has also recently been shown to occur in migrating finches (Lindström & Alerstam 1986).

The migration strategies described above are supported by short distance recoveries of Robins ringed earlier in the same autumn. Recoveries within about a 300 km radius from Falsterbo are all in SW Scania or in the Copenhagen area, i.e. in approximately the opposite direction to that of the true migration. Even if the recovery pattern may be biased by attraction to the birds from the illuminated cities of Malmö and Copenhagen (Persson 1972), it is obvious that relatively short northward autumn flights from Falsterbo are regular and may even include a majority of the Robins ringed at this site. Short-distance recoveries of Robins ringed at Ottenby indicate that the birds immediately continue their journey in the normal autumn migration direction (cf. Roos 1984, Sandberg et al. 1988). Also, recent orientation experiments on Robins from the two sites showed that the Falsterbo Robins oriented mainly in a westerly or northwesterly direction in autumn, while the Ottenby Robins showed a mean orientation towards the southwest and south (Sandberg et al. 1988).

There are similar differences in fat deposition between Robins from the two sites during spring migration. We suggest, that the Ottenby Robins in spring again are in a phase of relatively long-stage migration across the Baltic Sea, on their way to their (assumed) major breeding areas in NE Fennoscandia. The Robins captured at Falsterbo have landed after a much shorter sea crossing. They are also closer to their (assumed) major breeding areas in SW Fennoscandia and thus near the destination

TABLE 4. Mean fat deposits, mean body weight and mean length in juvenile (first year of life) Robins captured at Falsterbo and Ottenby Bird Observatories during parts of seasons 1986.

Autumn	*n*	*Fat*	*Weight*	*SD*	*Wing*	*SD*
1-10 Sep						
Falsterbo	154	1.31	15.83	0.86	73.10	1.78
Ottenby	10	2.40	15.40	0.84	73.00	1.83
t-test			n.s.		n.s.	
21-31 Oct						
Falsterbo	31	2.94	16.37	0.93	73.45	1.77
Ottenby	165	3.90	16.24	1.25	73.29	1.80
t-test			n.s.		n.s.	
Spring						
1-10 Apr						
Falsterbo	80	2.46	16.11	1.21	73.80	1.60
Ottenby	22	3.14	15.59	1.30	74.14	1.18
t-test			n.s.		n.s.	
1-10 May						
Falsterbo	89	3.11	16.05	1.11	71.85	1.47
Ottenby	376	3.30	14.94	1.20	72.01	1.44
t-test			0.001		n.s.	

of their spring migration, which could be a reason for carrying less fat.

Adults show patterns similar to those of juveniles, but sample sizes were rather small to allow adequate statistical comparisons (see Table 2).

DISCUSSION

The fact that Robins captured at Falsterbo are heavier but still carry less fat than their conspecifics at Ottenby is both unexpected and surprising. The two ringing sites are less than 300 km apart, and both are situated on southerly or southwesterly protruding points in the Baltic Sea. The sites are visited by migrating Robins from widely overlapping breeding and wintering areas according to ringing data (Roos 1984, Liljefors et al. 1985, Pettersson et al. 1986). Except for Robins from populations breeding in the Soviet Union, which occur at Ottenby during certain weather conditions in late autumn, the birds can be considered as belonging to the Fennoscandian population. It is likely, however, that the Robins captured at Falsterbo are recruited from the southwesterly part of this population to a greater extent than those caught at Ottenby, where most will have a more northeasterly origin.

Body weight

It has been assumed, in many earlier studies, that body weight is closely related to fat level. It is in this study too, if attention is restricted to birds captured at either one of the two sites, though this does not hold if birds from both sites are compared (cf. Fig. 1). The Falsterbo Robins are on average heavier within each age group and season than the Ottenby Robins are, in spite of the larger fat deposits in the Ottenby birds (cf. Table 1).

The weight differences between Falsterbo and Ottenby Robins in autumn are more pronounced in the lower fat classes (Fig. 3A). The underlying reasons can only be speculated upon, since no physiological studies have been made so far. A likely reason is that the weight differences are connected with the migration strategies described above. The Falsterbo Robins carry small or minimal fat reserves, and the high body weight in these birds may be caused by a large amount of water. Before or during long-stage migration flights, birds may undergo dehydration, and we speculate that the Falsterbo Robins have not done so. On the other hand, most Ottenby Robins are in a phase of long-stage migration when captured. The low weights of these birds in fat classes 0-3 would then be caused by combustion of fat reserves, and perhaps also by dehydration (including metabolic water from fat) during the migration flight (cf. Torre-Bueno 1978).

In spring birds there are similar differences, which may also be connected with migration strategies (see above). Also, orientation experiments during spring migration showed, that the Falsterbo Robins were more attracted towards the sunset (under clear sky) than the Ottenby Robins. Under simulated total overcast the Falsterbo Robins failed to show a significant orientation (Sandberg et al. 1988). This pattern may be related to the discussion about recruitment areas above.

Variations within seasons

In Table 4 some seasonal variations in fat and weight within and between the two capture sites are shown. There is a difference of about one fat class both at the beginning and at the end of autumn migration between the Falsterbo and Ottenby Robins, the latter carrying more fat. There are, however, no differences in mean body weight or mean wing length. More birds are captured at Falsterbo than at Ottenby in the beginning of September, while the contrary occurs in late October. The Robins captured at Falsterbo in early September carry very little fat and are probably of a rather local (Scania?) origin. It is also interesting that the Ottenby Robins from the same period, though the sample size is small, carry less fat (2.4) but are heavier (15.40 g) than the averages for the whole autumn (3.0 and 15.26 g respectively). It is likely that these early autumn birds at Ottenby are also of a rather local origin, showing a fat-weight relationship similar to the Falsterbo Robins.

Later in autumn, birds with more fat appear at both sites, and during the last ten days of October, the mean fat class in the Falsterbo Robins is 2.9, and in the Ottenby Robins 3.9. There are still no weight or wing length differences. These birds should, according to the discussion above, be of a more remote origin, carrying out longer-stage migration flights, especially at Ottenby.

Pettersson and Hasselquist (1985) suggested that Robins captured at Algutsrum, a woodland and pasture area about 60 km north of Ottenby, were in a late premigratory status. The birds were captured 1-21 October 1982. The mean fat class of these birds was 3.2 and their mean body weight was 16.56 g, significantly heavier than Robins captured at Ottenby during the same period (mean fat class 2.7, mean body weight 15.46 g). For comparison, these data from Algutsrum are included in Fig. 1. There is a clear similarity between the "short-stage migrants" captured at Falsterbo and the suggested premigratory, fat-accumulating birds at Algutsrum.

In spring, sample sizes show the same variation as in autumn, i.e. more Robins are trapped at Falsterbo in early April, more at Ottenby in early May. The birds captured 1-10 April have on average 2 mm longer wings than those captured 1-10 May at both sites, showing the earlier arrival of males in spring (cf. Pettersson 1983 b, Karlsson et al. 1986).

As in autumn the Falsterbo Robins carry less fat but are heavier than the Ottenby Robins. The largest weight difference occurs 1-10 May, when birds of almost the same fat class are on average 1 g heavier at Falsterbo.

It is apparent from this study, that body weight alone should not be used when estimating fat reserves and when calculating flight ranges. Furthermore, it is important to notice that the fat-weight relationship can vary considerably depending on the geographical location of the capture site and the migratory situation of the birds. The results shown here for the Robin is probably one example of many, and future work will be needed to discover if other species show similar patterns.

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