

Body composition and migration strategies: a comparison between Robins (*Erithacus rubecula*) from two stop-over sites in Sweden

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Robins captured as passage migrants by the Baltic Sea in South Sweden at Falsterbo and Ottenby Bird Observatories, respectively, differ with respect to body mass, fat load and orientation behaviour. Relatively more birds with large visual fat deposits are captured at Ottenby than at Falsterbo. However, comparing the body contents of birds of the same visual fat class and wing length, as reported in this study, shows that Robins at Falsterbo carry more fat than Robins at Ottenby. There is no difference in relative water content between birds from different fat classes, seasons or places. Robins with small fat loads at Ottenby probably consisted of birds which had depleted their fuel reserves during a preceding extensive flight across the Baltic Sea. Flight muscle mass and fat-free body mass of these birds were significantly reduced. In contrast, lean birds captured at Falsterbo had approximately the same fat-free body mass and flight muscle mass as birds with large fat reserves at Falsterbo as well as Ottenby. Birds may arrive at Falsterbo by migrating by successive short flights mainly over land. Relative liver mass was larger in Robins from Falsterbo than from Ottenby. The difference in fat content, fat-free body mass, flight muscle and liver mass may reflect differences in physiological and ecological conditions for Robins migrating mainly over land (arriving at Falsterbo) and over sea (arriving at Ottenby), respectively.

Key words: Robin (*Erithacus rubecula*), body composition, fat content, dehydration, migration strategies, Sweden.

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1. Introduction

The Robin (*Erithacus rubecula*) is a nocturnal migrant with its wintering range in the Mediterranean region (ROOS 1984, PETTERSSON et al. 1986). Spring migration in Sweden culminates in April and May and autumn migration peaks in September and October (HÖGSTEDT & PERSSON 1971, PETTERSSON 1983 a, 1983 b, ROOS 1984). It is captured in big numbers at both the Falsterbo and Ottenby Bird Observatories in southern Sweden during spring and autumn migration.

In autumn, Robins captured at Falsterbo migrate over land before arriving at Falsterbo. Especially on occasions with easterly winds during the autumn, many Robins of easterly origin are captured at Ottenby (PETTERSSON & LINDHOLM 1983, GEZELIUS & HEDENSTRÖM 1988). These Robins probably reach the Ottenby area after a non-stop flight across the Baltic Sea. Analyses of the orientation behaviour and the direction of short-distance recoveries a few days after ringing show a difference in migration behaviour between Robins from the two sites: SANDBERG et al. (1988) found that during autumn migration Robins at Ottenby continue their migration towards the south, while Falsterbo Robins undertake northerly movements. The authors concluded that the orientation differences might be due to the different preceding and impending migration circumstances, with respect to flights over land and sea, for the Falsterbo and Ottenby Robins, respectively, and to the body condition of the birds. The spring migration is less known (see PETTERSSON 1983 b, SANDBERG et al. 1988), but the situation

is probably similar to that in the autumn, i. e. the Ottenby birds are grounded after having carried out a much longer flight over the sea than the Falsterbo birds.

KARLSSON et al. (1988) investigated the fat-mass relationships in Robins captured at Falsterbo and Ottenby. They found that the Robins were of almost the same size at the two sites, but Robins captured at Falsterbo were heavier even if they were classified as containing less fat than Robins captured at Ottenby. The proposed explanation of these differences was that birds captured at the two sites use different migration strategies. The Robins at Falsterbo probably have used short-stage migration carrying relatively small fat deposits when migrating over land, while Ottenby Robins are mainly long-stage migrants carrying larger fat reserves when flying over the Baltic Sea (SANDBERG et al. 1988, KARLSSON et al. 1988). This explains why Falsterbo Robins have on average smaller fat reserves than Ottenby birds. But why do Falsterbo and Ottenby Robins of the same category with respect to the amount of visible fat, differ in body mass?

These are at least two different possible explanations for this difference: (1) Differences in body mass may reflect differences in water content. Dehydration may occur in Ottenby Robins which are grounded after an extensive flight over the Baltic Sea. This explanation was suggested by KARLSSON et al. (1988). (2) It is conceivable that the captures at Ottenby mainly reveal the condition of birds in the process of fuel consumption during long flights across the Baltic Sea. In contrast, many Falsterbo birds probably have carried out only short flights over land and during autumn they are probably in a phase of fuel deposition, building up their reserves before setting out on a sea crossing and continuing migration towards the winter range. Hence, the different fat: weight relationship between Falsterbo and Ottenby Robins may reflect an asymmetry in the change of body contents or in the way fat is stored in the body during multiple short flights and long sustained flights, respectively.

In order to test these two hypotheses about the differences in body mass and fat load between Robins captured at Falsterbo and Ottenby, we collected specimens from these two sites for analyses. Here we present the results from these analyses of body composition with respect to fat-free dry mass, fat and water contents. We have also compared the relative size of liver and flight muscles between birds from the two sites.

2. Methods

A sample of 38 Robins was collected for analysis during spring and autumn migration in 1988 and 1989, at Falsterbo (55.23 N, 12.49 E) and Ottenby (56.12 N, 16.24 E). All birds were juveniles of the same size (wing length 72 mm). Birds of two different fat classes (1 and 5, according to a seven-class scale for visual fat reserves as presented by PETTERSSON & HASSELQUIST 1985), and with a body mass close to the average for each place, were collected during the standard ringing procedure. At Falsterbo the average body mass of Robins in spring (autumn) in fat class one are 15.3 g (15.5 g) and in fat class five 17.6 g (17.4 g), respectively. At Ottenby the corresponding figures are 13.6 g (14.1 g) and 16.5 g (16.8 g) (KARLSSON et al. 1988). Unfortunately, it was not possible to obtain any birds with the stipulated wing length in fat class one during spring migration at Falsterbo.

Carcasses of the collected birds were immediately stored in a freezer (-18°C) until analysis. The bodies were dissected into three parts; liver, flight muscles (*M. pectoralis* and *M. supracoracoideus*) and remaining body, and treated separately. Fat mass, water content and the fat-free dry mass were determined by standard procedure (EVANS & SMITH 1975, PIERSSMA 1984). After dissection, carcasses were dried in an oven until constant dry mass was obtained after 72 hours. To measure the fat content a Soxhlet extractor was used during 24 hours with repeated washings in petroleum ether (b. p. $60-80^{\circ}\text{C}$). During the dissection procedure the total body mass decreased by on average 1.4%; this should be added to the total body mass in Table 1. For statistical testing MANN-WHITNEY U-test was used (SIEGEL 1956).

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3. Results

Mean values of total body mass (TBM), fat-free dry mass (FFDM), fat mass (FM), water mass (WM) along with associated standard deviations are given for each fat class during both spring and autumn in Table 1. Statistical comparisons are possible for data referring to fat class five during spring migration and fat class one and five during autumn migration. These three groups will be referred to as fat class S5, A1 and A5, respectively.

Table 1: Total body mass (TBM), body contents: fat-free dry mass (FFDM), fat mass (FM), water mass (WM), and numbers of Robins collected at Falsterbo (F) and Ottenby Bird Observatories (O) during spring and autumn migration 1988 and 1989. Masses are given in grams (g). Birds were sampled from two different fat classes, one and five, according to the visual scale for fat estimation by BUSSE & KANIA (1970) modified by PETTERSSON & HASSELQUIST (1985). Mean and standard deviations in each fat class during spring and autumn are shown as well as significance levels according to MANN-WHITNEY U-test (SIEGEL 1956).

Tab. 1: Körpermassa (TBM), fettfreie Trockenmasse (FFDM), Fettmasse (FM), Wassermasse (WM) und Anzahl gesammelter Rotkehlchen bei Falsterbo (F) und Ottenby (O). Es wurden Vögel der Fettklassen 1 und 5 untersucht (zur Einstufung vgl. BUSSE & KANIA 1970, modifiziert nach PETTERSSON & HASSELQUIST 1985). Für die zwei Fettklassen wurden getrennt nach Frühjahr und Herbst jeweils Mittelwert, Standardabweichung und Signifikanzniveau bei Anwendung des MANN-WHITNEY U-Tests (SIEGEL 1956) angegeben.

	Fat class and no. birds collected (F, O)	Total body mass (TBM)		Fat-free dry mass (FFDM)	
		Falsterbo	Ottenby	Falsterbo	Ottenby
Spring	1 (0,4)	—	12.5 (1.8)	—	4.1 (0.5)
Spring	5 (6,5)	16.8 (0.2) p<0.05	16.0 (0.9)	4.8 (0.1) n. s.	5.0 (0.3)
Autumn	1 (8,5)	14.6 (0.3) p<0.001	12.6 (1.1)	4.8 (0.1) p<0.001	4.2 (0.3)
Autumn	5 (5,5)	16.8 (0.2) n. s.	16.5 (0.5)	4.9 (0.2) n. s.	5.1 (0.2)
	Fat class and no. birds collected (F, O)	Fat mass (FM)		Water mass (WM)	
		Falsterbo	Ottenby	Falsterbo	Ottenby
Spring	1 (0,4)	—	0.4 (0.1)	—	8.0 (1.2)
Spring	5 (6,5)	2.5 (0.4) p<0.05	1.7 (0.4)	9.6 (0.4) n. s.	9.2 (0.8)
Autumn	1 (8,5)	0.7 (0.2) p<0.01	0.3 (0.2)	9.2 (0.3) p<0.01	8.1 (0.8)
Autumn	5 (5,5)	2.6 (0.7) n. s.	2.0 (1.2)	9.3 (0.5) n. s.	9.3 (1.3)

The differences in body contents between Robins captured at Falsterbo and Ottenby are most marked in fat class A1 (Tab. 1 and 2). Differences in total body mass (Tab. 1) reflect the fact that birds collected for analysis were selected so as to conform to the typical body mass for the respective site and fat class (cf. KARLSSON et al. 1988). On average, birds at Falsterbo are heavier (TBM) than birds at Ottenby in the same fat class, but considering FFDM the difference was statistically significant in fat class A1 only ($U = 0$, $p < 0.001$).

There was a significant difference in fat content between Falsterbo and Ottenby Robins in fat class A1 ($U = 1$, $p < 0.01$) and S5 ($U = 3$, $p < 0.02$) but not in fat class A5 ($U = 11$, $p > 0.42$,

Tab. 1). The ratio of fat to fat-free dry mass is significantly different in fat class A 1 and S 5 but not in A 5. The median values of this ratio are 12.6% in Robins of fat class A 1 at Falsterbo and 5.6% at Ottenby ($U = 3$, $p < 0.01$). In fat class A 5 the corresponding figures are 45.8% and 46.5%, respectively ($U = 11$, $p > 0.42$) and in fat class S 5 53.4% and 33.6% ($U = 1$, $p < 0.01$), respectively (Tab. 2).

Table 2: Median values and range (min-max) of percentage fat, as fat mass relative to fat-free dry mass (FM/FFDM), and percentage of water, as fraction water of fat-free wet mass (WM/FFWM), are shown. Significance levels according to MANN-WHITNEY U-test (SIEGEL 1956). See table 1 for further explanations.

Tab. 2: Median-Werte und Amplitude (Minimum-Maximum) für relativen Fettgehalt (Fettmasse FM/fettfreie Trockenmasse FFDM) und relativen Wassergehalt (Wassermasse WM/fettfreie Feuchtmasse FFWM).

	Fat class	% Fat (FM/FFDM)		% Water (WM/FFWM)	
		Falsterbo	Ottenby	Falsterbo	Ottenby
Spring	1	—	9.5 (8.2–17.2)	—	66.0 (61.1–67.4)
Spring	5	53.5 (53.1–57.8) $p < 0.01$	33.6 (23.4–48.4)	66.6 (65.5–68.0) $p < 0.01$	64.0 (63.7–66.0)
Autumn	1	12.6 (10.7–24.4) $p < 0.01$	5.6 (5.1–12.2)	66.2 (64.4–66.7) n. s.	65.6 (64.0–68.3)
Autumn	5	45.8 (42.3–82.0) n. s.	46.5 (15.0–64.7)	64.9 (64.4–66.7) n. s.	63.8 (61.7–67.8)

Percentage of water in the bodies, expressed as water of fat-free wet mass (Tab. 2), was about 65% and corresponds well with what is normally found in migrating birds (e. g. HELMS & SMYTHE 1969, MOREAU & DOLP 1970). Percentage of water did not differ between sites or fat classes (comparison between sites for fat class A 1: $U = 9$, $p > 0.06$, fat class A 5: $U = 8$, $p > 0.21$), except for fat class S 5 where the difference, although numerically small, was statistically significant ($U = 2$, $p < 0.01$). Comparing the total sample of Robins from Falsterbo and Ottenby there was no significant difference in amount of water ($U = 125$, $p > 0.10$).

Median and range for relative liver mass (liver FFDM/total FFDM) are shown for the different categories of Falsterbo and Ottenby Robins in Table 3. Generally, the liver was relatively heavier in Robins captured at Falsterbo than at Ottenby, irrespective of fat class ($U = 56$, $p < 0.002$).

Table 3: Median values and range (min-max) of relative liver mass, as liver fat-free dry mass of total fat-free dry mass (liver FFDM/total body FFDM, in percent) and median values and range of relative flight muscle mass (flight muscle FFDM/total body FFDM, in percent). See table 1 for further explanation.

Tab. 3: Median-Werte und Amplitude für relative Leber-Masse (fettfreie Leber-Trockenmasse liver FFDM/gesamte fettfreie Trockenmasse total FFDM, in %) und relative Flugmuskel-Masse (Flugmuskel FFDM/gesamte FFDM, in %).

	Fat class	Relative liver mass (liver FFDM/total FFDM) %		Relative flight muscle mass (flight muscle FFDM/ total FFDM) %	
		Falsterbo	Ottenby	Falsterbo	Ottenby
Spring	1	—	4.0 (3.5–4.9)	—	11.0 (6.1–11.7)
Spring	5	4.9 (4.5–6.2)	4.2 (3.5–4.7)	13.3 (12.2–14.2)	13.9 (12.6–14.5)
Autumn	1	4.6 (4.0–5.8)	3.8 (2.6–4.5)	12.2 (11.8–12.7)	9.7 (8.7–11.8)
Autumn	5	4.9 (4.5–5.5)	4.0 (3.0–0.6)	12.6 (10.7–13.7)	13.1 (11.6–13.6)

In Ottenby Robins the relative mass of the flight muscles (flight muscle mass FFDM/total FFDM), was greater in fat class five than in fat class one during both spring ($U = 0$, $p < 0.001$) and autumn migration ($U = 1$, $p < 0.01$, Tab. 3). In autumn there was no difference in relative flight muscle mass between Falsterbo Robins in fat class one and five ($U = 10$, $p > 0.08$).

Comparing Robins collected at Falsterbo and Ottenby, there was no difference in relative flight muscle mass between birds in S 5 ($U = 9$, $p > 0.16$) or A 5 ($U = 9$, $p > 0.27$) but there was a significant difference in the A 1 group (mean Falsterbo = 12.2%, mean Ottenby = 9.7%; $U = 0$, $p < 0.001$).

4. Discussion

Fat content

The difference in body mass between Robins making a stopover at Falsterbo and Ottenby, respectively, as demonstrated by KARLSSON et al. (1988) seems to be due both to differences in fat-free wet mass and fat mass. Comparing birds in the same visual fat class, this analysis shows that the Falsterbo Robins carry larger fat deposits than Ottenby Robins. Consequently, this difference in fat mass is not revealed by the visual scale for fat estimation. The observers had calibrated and tested their measuring procedure according to this scale and found no systematic differences between the two sites (KARLSSON et al. 1988). During the dissection procedure we observed differences between individuals in how the fat was distributed within the body, also in birds of the same fat class. However, it was not possible to quantify the observed variation in size of subcutaneous fat deposits and fat deposits inside the body cavity. Our results indicate that it is difficult to use the visual scale for accurate fat estimation and that one has to be cautious when comparing results from different areas.

The differences in fat content might reflect differences in deposition and use of energy reserves at Falsterbo and Ottenby. It is also possible that a greater proportion of Robins captured at Falsterbo are in the process of accumulating rather than consuming fat in comparison with Ottenby Robins. Birds accumulating fat may distribute their fat reserves differently than birds actively using their energy reserves, as suggested in hypothesis (2).

Water content and dehydration during migration

The results of this study show no substantial difference in relative water content between Robins with different fat deposits, neither between seasons nor sites. There was a small difference between Ottenby and Falsterbo Robins in fat class S 5 but when comparing all birds from the two sites, the difference between the two groups was no more significant. Consequently, we conclude that Robins captured at Falsterbo and Ottenby do not differ in dehydration as suggested in hypothesis (1).

Experiments with pigeons (BIESEL & NACHTIGALL 1987) and Starlings *Sturnus vulgaris* (TORRE-BUENO 1978) flying in windtunnels show that sustained flight causes water loss, when the ambient temperature exceeds 6–7 °C. As YAPP (1956, 1962) pointed out this indicates that water loss together with depleted fat reserves could be a limiting factor for long distance flights. The ambient temperature in nights during the migration season of Robins making landfalls at Ottenby and Falsterbo was between –3 °C and +10 °C in spring and between +5 °C and +15 °C in autumn according to local temperature registrations in 1989. At greater heights the temperature is even lower, because in the standard atmosphere temperature decreases by 6 °C for every 1000 m of increased height. Radar observations and observations from aircraft of nocturnal migrants over inland and coastal areas show that on average 90 % of the birds are flying below 1500–2000 m height and 50 % below 400–700 m (ALERSTAM 1977). We therefore conclude that dehydration in Robins is unlikely.

Body composition and migration strategies

In this study we found that the fat-free dry mass of lean birds at Ottenby (S1, A1) was on average lower than in Robins in any other category. Fat-free dry mass reflects the body size of a bird, and therefore the first objection may be that body sizes differ between birds captured at the two sites. Since fat-free dry mass of Robins in A5 and S5 do not differ between the two sites and the mean winglength is almost the same at the two sites (KARLSSON et al. 1988) this is probably not the case.

It has been suggested that the increase in flight muscle mass (FFDM) before migration may be an adaptation that compensates for the increased power requirements for flight by birds with heavy fuel loads (FRY et al. 1972, MARSH 1984). The increased muscle protein reserves may partly be used as energy metabolised during flight when the fat loads are depleted (PENNYCUICK 1975). In the present study we found a significant difference in relative flight muscle mass (FFDM) between birds with small and big fat loads only in Robins captured at Ottenby. The difference is interesting since Robins captured at Ottenby are thought to have undertaken the longest migration flights in autumn (PETTERSSON & LINDHOLM 1983, GEZELIUS & HEDENSTRÖM 1988), and lean birds may have used up some of their protein reserves in their flight muscles. In contrast, Robins migrating over land (Falsterbo) can travel by short flights without any great losses in fuel load and without metabolizing their protein reserves. The flight muscles of birds in fat class five were all of the same average size, irrespective of season or collecting site.

We found that the relative liver mass (FFDM) of Robins captured at Falsterbo was on average about 20% larger than that of Ottenby Robins. The liver is the major site for fatty acid synthesis and together with the muscles the main site for glycogen storage in birds (WHITROW 1986). An interesting contrast emerges if one considers the possibility that the difference in body contents between lean and fat Falsterbo birds (fat class 1 and 5) mainly reflects what happens during migration by multiple short flights, and that of Ottenby birds reflects what happens during fuel consumption in long sustained flights. The difference in total body mass between lean and fat Falsterbo birds can be assigned almost exclusively to a difference in the amount of stored fat. The fat-free body mass is virtually the same for fat and lean Falsterbo birds. Birds travelling by multiple short flights can rapidly replenish the small losses in fat and protein reserves associated with each flight during stopover intervals. In contrast, at Ottenby lean birds not only have a smaller amount of fat but their fat-free body mass is clearly reduced in comparison with that of fat birds. Of the difference in total body mass between fat and lean Ottenby birds, about 40% are due to differences in the amount of fat mass and 60% to differences in the mass of fat-free tissues (including flight muscles). This indicates that fat consumption during long flights is associated with a simultaneous loss of fat-free tissue (cf. PIERSMA & VAN BREDENRODE 1990, PIERSMA & JUKEMA 1990).

We conclude that the differences in fat content and body and flight muscle mass between Robins captured at Falsterbo and Ottenby together with differences in orientation behaviour and short-distance recoveries (SANDBERG et al. 1988) may reflect a different migration pattern between Robins making a landfall at Falsterbo and Ottenby, related to the birds' preceding migration flights over land and sea, respectively.

5. Zusammenfassung

Fettreserve, Flugmuskelmasse und Lebergröße als Parameter des Zugverhaltens: Vergleich zwischen Rotkehlchen (*Erithacus rubecula*) von zwei Rastplätzen in Schweden.

Rotkehlchen-Durchzügler, die im Süden Schwedens auf Falsterbo bzw. Ottenby gefangen wurden, unterscheiden sich in Körpermasse, Fettreserven und Zugverhalten. Bei Ottenby wurden relativ mehr

Vögel mit äußerlich erkennbarem großen Fettdepot gefangen als bei Falsterbo. Vergleicht man jedoch nur Vögel gleicher Fettdepot-Einstufung und gleicher Flügelänge (wie in der vorliegenden Arbeit geschehen), zeigt sich, daß Falsterbo-Rotkehlchen fatter als Ottenby-Vögel sind. Im relativen Wassergehalt existiert zwischen Rotkehlchen verschiedener Fett-Kategorien, zwischen Herbst- und Frühjahrsfänglingen und zwischen Individuen der beiden Fangplätze kein Unterschied. Ottenby-Rotkehlchen mit nur geringem Fettdepot sind wahrscheinlich Vögel, deren Fettreserven durch den vorausgegangenen Flug über die Ostsee verbraucht wurden. Auch die Flugmuskelmasse und die fettfreie Körpermasse waren bei letzteren signifikant reduziert. Dagegen hatten magere Falsterbo-Fänglinge eine ungefähr gleichgroße fettfreie Körpermasse und Flugmuskul-Masse wie Rotkehlchen mit großen Fettreserven sowohl bei Falsterbo als auch bei Ottenby. Wandernde Rotkehlchen dürften Falsterbo vor allem mit sukzessiven kurzen Flügen über Land erreichen. Im Vergleich zu Ottenby-Vögeln hatten die Falsterbo-Rotkehlchen eine relativ große Leber. Die Unterschiede in Fettreserven, fettfreier Körpermasse, Masse des Flugmuskels und der Leber zwischen Falsterbo- und Ottenby-Vögeln dürften die unterschiedlichen physiologischen und ökologischen Bedingungen während des Zugverhaltens widerspiegeln (Erreichen vom Falsterbo vorwiegend durch Zug über Land, von Ottenby durch Zug über die Ostsee).

6. References

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