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Fat loads and estimated flight–ranges in four *Sylvia* species analysed during autumn migration at Gotland, South–East Sweden.

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The migratory capacity of four Sylvia species was investigated during their initial phase of autumn migration in Sweden. Fat loads of individual birds were estimated by first determining approximately the fat–free body masses for birds of different size (as judged from body mass – fat index relationships). Individual fat loads varied considerably both inter– and intra-specifically. The mean fat load (% fat mass of total body mass) of different species was: Lesser Whitethroat 9.3%, Whitethroat 7.2%, Garden Warbler 16.4% and Blackcap 13.2%. Comparatively low fat loads in the first two species may be because they probably commence their autumn migration in this area before the post–juvenile moult is completed. Our results indicate that several autumn migrating Garden Warblers and Blackcaps stopping over at Gotland have the energetic capability to almost cross continental Europe without refuelling This contrasts with the Whitethroat and the Lesser Whitethroat of which many individuals would only be able to cross the Baltic Sea.

Avian migration requires extra energy for flight. For a long time it has been known that migratory birds can store large amounts of fat as fuel (e.g. Odum and Connell 1956, Odum 1960, Nisbet *et al.* 1963, King and Farner 1965, King 1972). In some cases, especially before flights over large inhospitable areas, they can almost double their body mass by means of fat storage (Nisbet *et al.* 1963, Fry *et al.* 1970, Bibby and Green 1981, Alerstam 1982). Migration is normally divided into several flight periods and between these periods the birds have to replenish fat stores at suitable stop–over sites. Accumulated fat loads are probably a trade–off between several costs and benefits (e.g. migration speed, food resources and predation risk), a situation that has been used to construct theoretical models for optimal bird migration (Alerstam and Lindström 1990). Analyses of fat loads at stop–over sites along the migration route may thus be useful for characterizing migration strategies (e.g. Odum 1958, Blem 1980, Bibby and Green 1981, Alerstam 1982, Lindström 1987).

Fat loads can be determined or estimated by different methods. The most accurate way is to extract the lipid contents from the carcasses of bird corpses (e.g. Odum and Perkinson 1951), but this method is hardly applicable in large field studies. Another, more commonly used, approach is to estimate the visible amount of subcutaneous fat on living birds. The amount of fat can be classified according to an index scale, several of which have been suggested (e.g. McCabe 1943, Helms and Drury 1960, Busse and Kania 1970, Pettersson 1983). Although offering several advantages over the lipid extraction procedure, the fat index classification has a drawback in that it does not give direct information about the actual fat load, a parameter necessary for estimates of potential flight–ranges. Ellegren (1989) has recently reported a method which allows the estimation of fat load from values of body mass and wing length, without prior calibration by the lipid extraction procedure (see also Pettersson & Hasselquist 1985 and Hedenström & Pettersson 1986). This method

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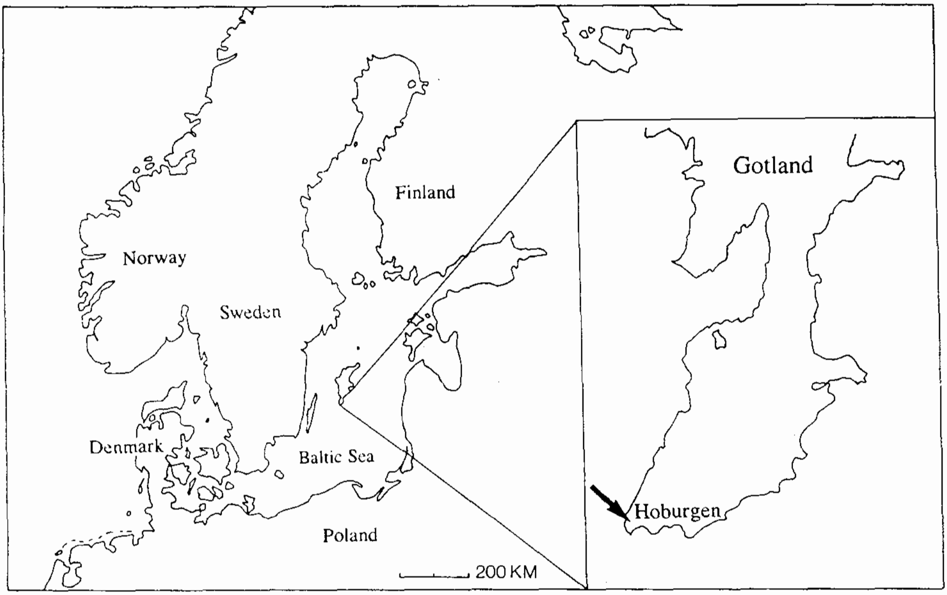

Figure 1. Map showing the Baltic Sea and the location of the trapping site (indicated by arrow) at the southernmost point of Gotland.

approximates the size-specific fat-free body mass as the body mass of birds with no visual subcutaneous fat.

We have estimated the fat loads in four warblers of the genus *Sylvia* during their initial phase of autumn migration at Gotland, South-East Sweden. We have also tried to estimate the flight ranges that individual birds would be able to cover with the observed fat loads. The four species concerned are the Lesser Whitethroat *Sylvia curruca,* the Whitethroat *S.communis,* the Garden Warbler *S.borin* and the Blackcap *S.atricapilla.* With exception of the Blackcap, the north European populations of these warbler species are exclusively trans-Sahara migrants (Zink 1975). North-European populations of the Blackcap have a complicated migratory pattern with wintering areas in middle and southeast Europe as well as in tropical East Africa (Zink 1975, Fransson unpubl.)

MATERIAL AND METHODS

Field work

Body mass and size data have been gathered during regular bird ringing of migrants at Hoburgen 5655'N 18°08'E, the southernmost point of the island Gotland in the Baltic Sea (see Figure 1). Here, bird ringing has been carried out by the Sundre Bird Ringing Group during parts of the spring and autumn since 1976 (see Fransson & Mellroth 1988). Data used in this analysis were sampled during the autumns of 1986, 1987 and 1988, during the period 25 July - 10 October. The trapping site is situated close to the sea-border in an area with sparse vegetation of small bushes, mainly the Whitebean *Sorbus intermedia* and the Dog-rose *Rosa canina.*

Between 15 and 25 mist-nets were used and the daily trapping started before sun-rise and lasted for at least 5 hours. Trapped birds were carried in bags to a small laboratory where they were ringed, weighed and measured. Data were collected by different bird ringers, who had been trained together. Age determinations followed Svensson (1984). Wing-length was measured according to method 3 of Svensson (1984), to the nearest mm. Body mass was determining using a Pesola spring balance with an accuracy of 0.1g. The sample sizes were: Lesser Whitethroat n = 321, Whitethroat n = 436, Garden Warbler n = 729 and Blackcap n = 147. About 93% of the birds were juveniles. Age groups were pooled in the estimations of fat–free body mass.

Estimates of fat loads

The amount of subcutaneous fat on the belly was classified as described by Pettersson (1983), i.e. using a fat index scale from zero (no visible fat) to six (extensive fattening on the abdomen and in the furcular cavity). The relationship between fat index and the average body mass within each fat index class, irrespective of size, for the different species are shown in Figure 2a–d. Estimates of fat loads followed Ellegren (1989). Birds were divided into groups with common wing–lengths (one value of wing–length in each group). Only groups consisting of at least twelve individuals (arbitrarily set) were taken into consideration. For each group body mass was related to fat index by a linear regression. From the numeric relationship obtained, the body mass corresponding to fat index zero was taken as a first estimate of the fat–free body mass for birds of the particular wing–length. The estimated value of the fat–free body mass for each wing–length of the species were then related to the corresponding wing–lengths by a second linear regression. This step was done in order to sharpen the estimates and to be able to estimate the fat–free body mass for wing–length classes outside the original interval. Size–specific fat–free body masses derived from the second linear regression were used to estimate the fat load of individual birds. This was simply done according to:

Fat load (% of total body mass) = (Total body mass – appropriate fat–free body mass/total body mass) x 100. We thus used the entire mass above the fat–free mass as an estimator of fat mass (cf. Piersma 1990).

Estimates of flight ranges

The distances that individual birds would be able to cover were calculated according to Pennycuicks' (1975) formula no.1. In the calculations we only used one value of wing–span for each species. All flight range estimates refer to still air conditions.

RESULTS

Body mass in relation to capture time

Birds in this study were captured between 04.00hr and 13.00hr. Linear regressions of capture time and body mass did not reveal any general mass increase within this time interval (Lesser Whitethroat r = 0.02, t = 0.33; Whitethroat r = 0.005, t = 0.11; Garden Warbler r = 0.01, t = 0.37; Blackcap r = 0.04, t = 0.53; all NS). Hence, we find no evidence for a daily time component in body mass variation. This was an important observation since the fat load estimates are based on the assumption that mass variations in birds of a given size purely reflect the fat status (but see Discussion).

It should be noted that the lack of mass increases during the day was not due to the counteracting effect of smaller birds being caught later in the day than larger birds (cf. Hedenström & Pettersson 1986). This was excluded by linear regressions of capture time and wing–length, which did not reveal any significant relationships (Lesser Whitethroat r = 0.02, t = 0.42; Whitethroat r = 0.07, t = 1.49; Garden Warbler r = 0.07, t = 1.78; Blackcap r = 0.14, t = 1.65; all NS).

Estimates of fat–free body masses

In Figure 3a–d, estimates of the fat-free body mass are shown for individual wing length classes of the four species. The final estimates of the fat–free body mass for birds of different wing lengths are listed in Table 1. Estimates are given for all classes of wing–length occurring in our sample, i.e. for classes with less than twelve individuals estimates were derived by extrapolations from the regression lines. The fat–free body mass ranged from 10 to 11g in the Lesser Whitethroat, from 13 to 14g in the Whitethroat, from 14 to 17g in the Garden Warbler, and from 14 to 18g in the Blackcap.

It should be noted that the average mass increase per mm wing length approximately correlated to the size of species. For the two smaller species, the Lesser Whitethroat and the Whitethroat, the mass increased with 0.13 and 0.11 gram, respectively, per mm wing length. The corresponding value for the Garden Warbler was 0.35 and for the Blackcap 0.32.

Fat loads

Summary statistics for the fat loads of the four species are given in Table 2 and the frequency distributions are shown in Figure 4a–d. The highest fat loads were found in the Garden Warbler and in the Blackcap. The Lesser Whitethroat and the Whitethroat had smaller

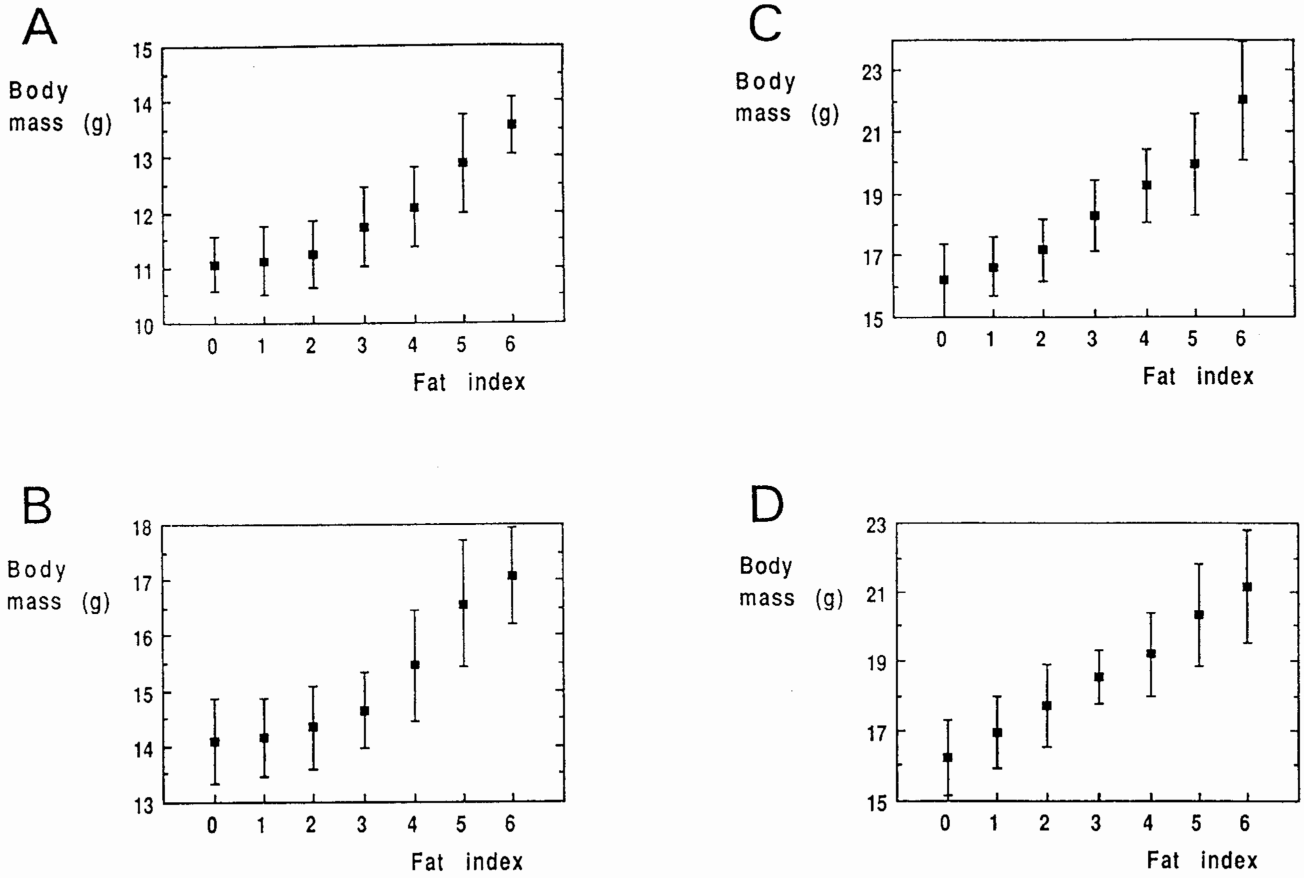

Figure 2. Relationships between fat index and the corresponding average body mass in the different *Sylvia* species analysed on autumn migration at Gotland, SE Sweden: (A) Lesser Whitethroat; (B) Whitethroat; (C) Garden Warbler; and (D) Blackcap. Bars show standard deviations.

Table 1. Estimated size-specific values of the fat-free body mass (g) in four *Sylvia* species analysed during autumn migration at Gotland, SE Sweden. Estimates were made according to Ellegren (1989).

Wing length (mm)	*Lesser Whitethroat*	*Whitethroat*	*Blackcap*	*Garden Warbler*
63	10.0			
64	10.1			
65	10.3			
66	10.4			
67	10.5			
68	10.7	13.0		
69	10.8	13.1		
70	10.9	13.2		
71		13.3	14.2	
72		13.4	14.5	
73		13.5	14.9	
74		13.6	15.2	
75		13.7	15.5	13.8
76		13.8	15.8	14.2
77			16.1	14.5
78			16.5	14.9
79			16.8	15.2
80			17.1	15.6
81			17.4	15.9
82			17.7	16.2
83				16.6
84				16.9

fat loads, for example, the proportion of individuals with a fat load less than 10% was 57% in the Lesser Whitethroat and 70% in the Whitethroat, compared to 20% in the Garden Warbler and 35% in the Blackcap. When the average fat load was calculated for the 25% fattest fraction of individuals (see Alerstam & Lindström 1990 for the logic behind this approach), values between 15.6% (Whitethroat) and 26.1% (Garden Warbler) were observed. The maximum estimated individual fat load in the different species varied between 27.7% (Lesser Whitethroat) and 43.0% (Garden Warbler). As a consequence of the approximations made, a few individuals had a negative fat load.

Comparisons between the fat load of adult and juvenile birds did not reveal any significant difference in the Whitethroat ($\bar{x}_{ad}$=8.0%, n=28; $\bar{x}_{juv}$=7.2%, n=408; t=0.65, NS), nor in the Garden Warbler ($\bar{x}_{ad}$=15.0%, n=70; $\bar{x}_{juv}$=16.6%, n=661; t=1.57, NS). In the Lesser Whitethroat adult birds had significantly higher fat loads than juvenile birds ($\bar{x}_{ad}$=15.9%, n=7; $\bar{x}_{juv}$=9.2%, n=311; t=2.62, $P<0.01$). In the Blackcap there were not enough adult birds to allow for testing. The mean fat load of male (n=67) and female (n=76) Blackcaps did not differ significantly (12.8% vs 13.9%, t=0.82, NS).

For the Garden Warbler and the Blackcap fat load of individual birds were not correlated, positively or negatively, to the progress of the autumn (r=0.03, t=0.84; r=0.10, t=1.25, both NS; 1 July = Day 1). In the Lesser Whitethroat (r=0.14, t=2.47, P=0.01) and in the Whitethroat (r=0.28, t=5.95 $P<0.001$), however, there was a significant positive correlation between fat load and the progress of the autumn. For example, the average fat load of juvenile Whitethroats changed from 4.9% (n=27) during the last days in July to 9.8% (n=55) in the beginning of September. The corresponding values for juvenile Lesser Whitethroats were 8.9% (n=47) and 12.7% (n=22).

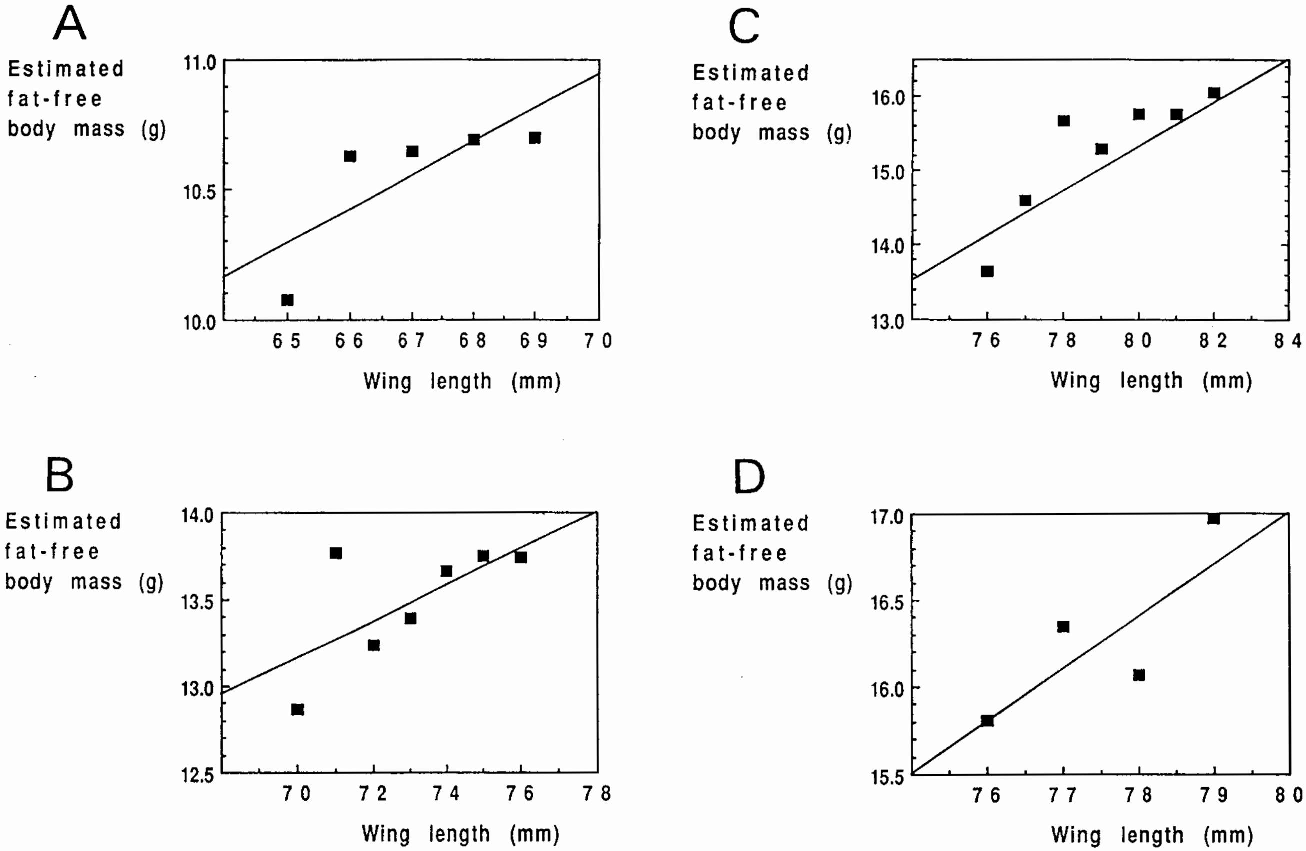

Figure 3. The relationship between wing length and estimated fat-free body mass in four *Sylvia* species analysed on autumn migration at Gotland, SE Sweden: (A) Lesser Whitethroat; (B) Whitethroat; (C) Garden Warbler; and (D) Blackcap.

Flight–range estimates

Estimated fat loads for individual birds were used to calculate possible flight–ranges. The Garden Warbler had the longest predicted mean flight–range whereas the Whitethroat had the shortest (Table 3). The proportion of individuals within each species that would be able to fly at least 300km (roughly one nights flight) was 57% in the Lesser Whitethroat, 47% in the Whitethroat, 92% in the Garden Warbler and 82% in the Blackcap. Figures 5 a–d show how the estimated flight–ranges with Gotland as the starting point turn out on the map. As evident from Figure 5, a considerable proportion of the Lesser Whitethroats and the Whitethroats are not able to reach the southern border of the Baltic Sea in still air. On the contrary, among Garden Warblers and Blackcaps a large proportion of the individuals would have the energetic capacity to reach central Europe with the current fat load. The mean flight range for the 25% fattest fraction of individuals in the Garden Warbler indicate that these birds would be able to reach as far as the northern parts of Italy. Moreover, in the Garden Warbler, seven individuals (1% of the sample) had predicted flight ranges between 2400 and 2800km, i.e. the distance to North Africa.

DISCUSSION

Methodological aspects on the fat load estimates

In this study we have estimated the fat load of living birds on the basis of their body mass when wing–length has been compensated for. Our methodological approach relies on two main assumptions whose validity we will first discuss.

(a) The fat–free body mass of birds of a given size (in this case indicated by wing–length) should be more or less constant within a species. (b) The body mass of birds with no visible subcutaneous fat should be a reliable estimator of the fat–free body mass for birds of a given size. However, since the sample sizes for birds classified to fat index 0 generally were small in the present study, we used linear

Table 2. Estimated fat loads (% of total body mass) in four *Sylvia* species analysed during autumn migration at Gotland, SE Sweden.

Species	*n*	*Mean*	*s*	*Mean of the 25% fattest fraction*[1]	*Maximum fat load*
Lesser Whitethroat	321	9.3	6.7	17.8	27.7
Whitethroat	436	7.2	6.5	15.6	28.2
Garden Warbler	736	16.4	7.8	26.1	43.0
Blackcap	149	13.2	7.9	23.3	32.7

[1] See Alerstam & Lindström (1990)

Table 3. Estimated flight–ranges[1] (km) in four *Sylvia* species analysed during autumn migration at Gotland, SE Sweden.

Species	*n*	*Mean*	*S*	*Mean of the 25% fattest fraction*[2]	*Maximum flight–range*
Lesser Whitethroat	321	400	270	770	1270
Whitethroat	436	340	280	730	1400
Garden Warbler	736	870	480	1520	2800
Blackcap	149	700	450	1330	1980

[1] According to Pennycuick (1975)
[2] See Alerstam & Lindström (1990)

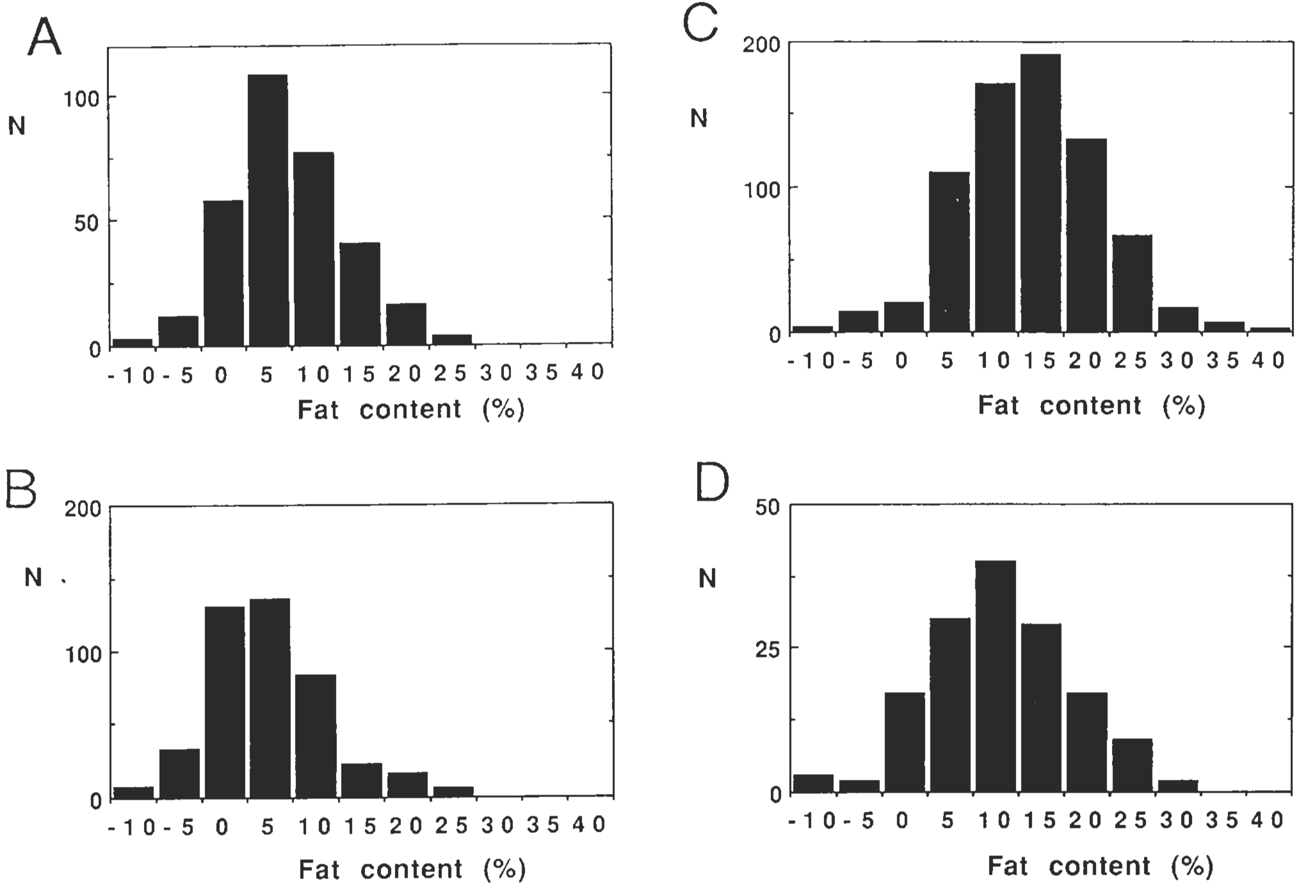

Figure 4. Frequency distributions of estimated individual fat loads in four *Sylvia* species analysed on autumn migration at Gotland, SE Sweden: (A) Lesser Whitethroat; (B) Whitethroat; (C) Garden Warbler; and (D) Blackcap. The fat load is divided into 5% classes. The figures given on the x axis represent the lower limit of each class.

Flight–range estimates

regressions of fat index and body mass in order to obtain mass values corresponding to fat index 0. This approach requires that the fat index/body mass relationship should be approximately linear.

Regarding the first assumption, several laboratory studies have shown that the fat–free body mass of small migrating birds of a given size does not vary between different sex or age classes (see e.g. Odum *et al.* 1964, Rogers & Odum 1964, and Child 1969). Some investigators have found small variations in the fat–free body mass between individuals of the same sex and age, variations that can be ascribed to varying water contents (e.g. Moreau & Dolp 1970). However, relatively constant fat–free body masses have also been observed, and the water content has been shown to not depend on, for example, the fat load by Connell *et al.* (1960) and Rogers & Odum (1964). We are aware of that the assumption of equal fat–free body masses for birds of a given size should be treated as a rough approximation.

It should also be noted that the fat–free body mass is known to differ intraspecifically due to several physiological and environmental factors (see e.g. Ormerod and Tyler 1990). Of these factors, the physiological stage, e.g. breeding, moult and migration, is of great importance. In our samples, however, almost all Garden Warblers and Blackcaps could probably be characterized as being in a pure migratory condition because they (a) carry significant amounts of visible fat; (b) show no sign of moult; (c) are rarely retrapped; and (d) do not breed in large numbers in the surrounding areas. Moult scores were not recorded in this study, but data from 1989 indicate that, among the very first arriving Lesser Whitethroats and among all Whitethroats, a significant proportion of the juvenile birds have still not accomplished by the post juvenile body moult (Fransson unpublished). Our preliminary data suggest that juvenile moulting Whitethroats are 0.5g heavier than non–moulting birds classified to the same fat index. Similarly, in a study in England, individuals of all these *Sylvia* species showed comparatively high body masses during the mid–moult period (Norman 1990). This suggests that the fat loads of some Lesser Whitethroats and Whitethroats (moulting birds) may be even less than our estimates indicate.

The second main assumption deals with the body mass of apparently fat–free birds (classified to index 0) as an estimate of the fat–free body mass. This is an approximation that does not for example, pay regard to internal fat that would have been detected in lipid extraction analysis (but whose significance as fuel for flight can be questioned). Consequently, a bird classified as fat index 0 may consist of some few percent extractable fat, but we consider this possible discrepancy as negligible for the purpose of this study.

Regarding a linear relationship between fat index and body mass, this has been reported for most species investigated (e.g. Pettersson & Hasselquist 1985, Ellegren 1989). This was also evident in this study for the Blackcap and the Garden Warbler (Figure 2c–d), but for the Lesser Whitethroat and the Whitethroat relationships tended to curve towards higher body masses in the lowest fat index region (Figure 2a–b). The divergence from linearity was probably a consequence of, again, heavier moulting individuals which carry less fat than birds with moult accomplished (Fransson unpublished).

Ecological aspects on the fat loads and the flight range estimates

By necessity, flight range estimates have been made without knowledge whether the birds were about to depart with their existing fat loads. Our samples thus probably contain a mixture of birds being in different migratory states, e.g. newly arrived birds, birds at stopover, birds just about to depart and birds not prepared for migration. As shown by Alerstam & Lindström (1990) we have calculated the average fat load of the 25% fattest proportion of individuals to derive an additional measure of the departure fat load

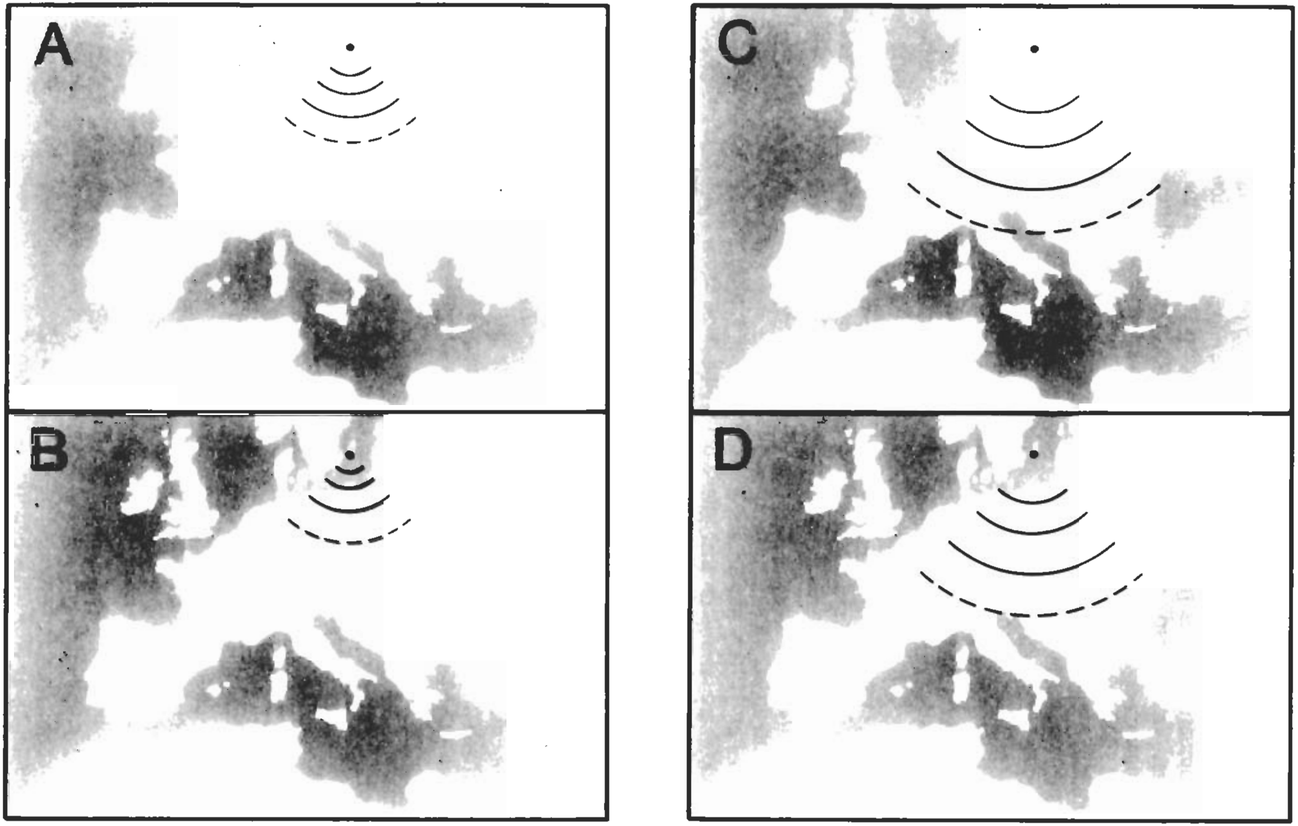

Figure 5. Estimated flight ranges with Gotland as the starting point. The three solid half circles represent the distance that 75%, 50% and 25% of the birds would be able to reach with the estimated fat loads, respectively. The broken half circles indicate the average flight range calculated for the 25% fattest fraction of individuals. (A) Lesser Whitethroat; (B) Whitethroat; (C) Garden Warbler; and (D) Blackcap.

and the flight capacity. Using this approach we obtained average flight–ranges between 730 (Whitethroat) and 1520km (Garden Warbler; see Tables 2 and 3, Figure 5a–d). These *Sylvia* species are thought to perform their migratory movements normally during nocturnal flights. Assuming a still air flight speed of about 35 km/h (Pennycuick 1975, Alerstam 1982) and a nocturnal flight period of eight hours, a bird would be able to cover a distance of approximately 300 km during one night. Still referring to the 25% fattest fraction, Garden Warblers and Blackcaps may have four to five nights flight capacity when they start from Gotland. This would enable them to almost cross the European continent without refuelling. In contrast, the 25% fattest proportion of the Lesser Whitethroats and the Whitethroats may only have capacity for two flight nights. Moreover, several Whitethroats did not have capacity for one whole nights flight, a capacity probably necessary for crossing the Baltic Sea (heading for Poland, a distance of about 250km). Unless these individuals do not orientate towards the Swedish mainland, this suggests that they have to accumulate more fat before they can move further. But again it should be emphasized that the flight range estimates refer to still air conditions, and usage of tail–winds could of course compensate small fat loads.

Clearly, our data demonstrate interspecific differences in accumulated fat loads and possible flight ranges in four *Sylvia* species analysed at Gotland. Does this imply that these species use different migration strategies? As mentioned, Lesser Whitethroats and Whitethroats still in post–juvenile moult appear at the trapping site. We do not know to what extent they represent locally moving birds or actually migrating birds. Both the Lesser Whitethroat and the Whitethroat have a positive correlation between the fat load and the progress of the autumn, a situation not found in the two other species. This can be interpreted as an increasing number of migrating Lesser Whitethroats and Whitethroats appearing at the trapping site asthe autumn progress. But even individuals caught late in the season have relatively low fat loads compared to the Garden Warbler and the Blackcap. Furthermore, there is a possibility that juvenile Lesser Whitethroats and Whitethroats commence their autumn migration in this part of Scandinavia before the moult has been accomplished. If so, simultaneous moult and migration may imply that juvenile birds migrate relatively slowly (and thus carry small fat loads) until the moult has been completed. Interestingly, Boddy (1983) has shown that juvenile Whitethroats regularly start their autumn migration in England before moult is completed. A similar pattern has also been found among Bluethroats *Luscinia s. svecica* in Sweden (Lindström *et al.* 1985) and Willow Warblers *Phylloscopus trochilus* in England (Norman 1981). In Bluethroats, simultaneous moult and migration may be one of the reasons why juvenile birds migrate at a more leisurely speed than adult conspecifics during the initial phase of autumn migration (Ellegren 1990).

Finally, we note that there should not be any large inhospitable area to pass during migration from Gotland towards the Mediterranean area. Under such conditions migratory birds are thought to use only moderate fat loads, since this is the most effective use of energy (see Pennycuick 1975, Alerstam & Lindström 1990). Alerstam & Lindström (1990) compared the departure fat loads for different categories of birds when passing over favourable areas. Using data from the 25% heaviest fraction of birds, a median fat load of 19% was revealed for 28 long–distance migrants. Our results are fairly close to this figure, but also show that among Garden Warblers and Blackcaps some individuals carry extensive fat loads even when flying over favourable areas.

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REFERENCES

Alerstam, T. (1982) Fågelflyttning. Signum. Lund.

Alerstam, T. and Lindström, Å. (1990) *Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner, E. (ed.) Physiological and Ecophyysiologiccal Aspects of Bird Migration. Springer–Verlag, Heidelberg.* pp. 331–351.

Blem, C.R. (1980) *The energetics of migration.* In: Gautreaux, S.A.Jr. (ed). Animal Migration, Orientation and Navigation.Academic Press, London and New York. pp. 175–224.

Bibby, C. and Green R.E. (1981) Autumn migration strategies of Reed and Sedge Warblers. *Ornis Scand.*, 12, 1–12.

Boddy, M. (1983) Factors influencing timing of autumn dispersal or migration in first–year Dunnocks and Whitethroats. *Bird Study,* **30,** 39–46.

Busse, P. and Kania, W. (1970) Operation Baltic 1961–1967 working methods. *Acta Orn.*, **12,** 231–267.

Child, G.I. (1969) A study of nonfat weights in migrating Swainson's thrushes (Hylocichla ustulata). *Auk,* **86,** 327–338.

Connell, C.E. Odum, E.P. and Kale, H. (1960) Fat–free weights of birds. *Auk,* **77,** 1–9.

Ellegren, H. (1989) Weight and wing–length as indicator parameters for accumulated fat levels in migrating birds – a methodological study of autumn migrating Bluethroats. *Vår Fågelvärld,* **48,** 75–85. (In Swedish with English summary).

Ellegren, H. (1990) Autumn migration speed in Scandinavian Bluethroats *Luscinia s. svecica. Ring. & Migr.,* **11,** 121–131.

Fransson, T. and Mellroth, R. (1988) Sundregruppens verksamhet 1987. *Bläcku,* **14,** 3–14. (In Swedish)

Fry, C.H., Ash, J.S. and Ferguson–Lees, I.J. (1970) Spring weights of some Palaearctic migrants at Lake Chad. *Ibis,* **112,** 58–82.

Hedenström, A. and Pettersson, J. (1986) Differences in fat deposits and wing pointedness between male and female Willow warblers caught on spring migration at Ottenby, SE Sweden. *Ornis Scand.,* **17,** 182–185.

Hedenström, A. and Pettersson,J. (1987) Migration routes and wintering areas of Willow Warblers *Phylloscopus trochilus* (L.) ringed in Fennoscandia. *Ornis Fenn.,* **64,** 137-143.

Helms, C.W. and Drury, H. (1960) Winter and migratory weight and fat field studies on some North American Buntings. *Bird–Banding,* **31,** 1–40.

King, J.R. and Farner, D.S (1965) Studies of fat deposition in migratory birds. *Ann. NY. Acad. Sci.,* **131,** 422–440.

King, J.R. (1972) *Adaptive periodic fat storage by birds.* Proc. XV Intern. Ornithol. Congr. pp.200–217.

Lindström, A., Bensch, S. and Hasselquist, D. (1985) Autumn migration strategy of young Bluethroats, *Luscinia svecica. Vår Fågelvärld,* **44,** 197–206. (In Swedish with English summary).

Lindström, A. (1987) *Fat deposition in migrating birds.* Introductory paper no 44, Department of Ecology, Lund University.

McCabe, T.T. (1943) An aspect of collectors' technique. *Auk,* **60,** 550–558.

Moreau, R.E. and Dolp, R.M. (1970) Fat, water, weights and wing–lengths of autumn migrants in transit on the northwest coast of Egypt. *Ibis,* **112,** 209–228.

Nisbet, I.C.T., Drury, W.H. and Baird, J. (1963) Deposition and consumption of fat by the Blackpoll Warbler *Dendroica striata. Bird Banding,* **34,** 107–138.

Norman, S.C. (1981) A study of the post–juvenile moult in Willow Warblers. *Ring. & Migr.,* **3,** 165–172.

Norman, S.C. (1990) A comparative study of post–juvenile moult in four species of *Sylvia* warbler. *Ring. & Migr.,* **11,** 12–22.

Odum, E.P. 1958. The fat deposition picture in the White-throated Sparrow in comparison with that in long–range migrants. *Bird Banding,* **29,** 105–108.

Odum, E.P. (1960). *Lipid deposition in nocturnal migrant birds.* Proc. XII Intern. Ornithol. Congr.pp. 563–576.

Odum, E.P. and Connell, C.E. (1956). Lipid levels in migrating birds. *Science* **123,** 892–894.

Odum, E.P. and Perkinson, J.D. Jr (1951) Relation of lipid metabolism to migration in birds. Seasonal variation in body lipids of the migratory White–crowned Sparrow. *Physiol. Zool.,* **24,** 216–230.

Odum, E.P., Rogers, D.T. and Hicks, D.L. (1964) Homeostasis of the nonfat components of migrating birds. *Science,* **143,** 1037–1039.

Ormerod, S.J. and Tyler, S.J. (1990) Assessments of body condition in Dippers *Cinclus cinclus:* potential pitfalls in the derivation and use of condition indices based on body proportions. *Ring. & Migr.,* **11,** 31–41.

Pennycuick, C.J. (1975) *Mechanics of flight.* In: Farner, D.S. and King, J.R. (eds). Avian Biology, Vol. V. Academic Press, London and New York, pp. 1–75.

Pettersson, J. (1983) *Åldersbestämning av tättingar och vadare (2 ed.).* Special report from Ottenby Bird Observatory No.1, Degerhamn.

Pettersson, J. and Hasselquist, D. (1985) Fat deposition and migration capacity of Robins *Erithacus rubecula* and Goldcrest *Regulus regulus* at Ottenby, Sweden. *Ring. & Migr.,* **6,** 66–76.

Piersma, T. (1990) Pre–migratory "fattening" usually involves more than the deposition of fat alone. *Ring. & Migr.,* **11,** 113–115.

Rogers, D.T. and Odum, E.P. (1964) Effect of age, sex and level of fat deposition on major body components in some wood warblers. *Auk,* **81,** 505–513.

Svensson, L. (1984) *Identification Guide to European Passerines.* 3rd edition, Stockholm.

Zink, G. (1975) *Der Zug europäischer Singvogel.* 1. Lfg.Vogelzug–Verlag, Moeggingen.

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