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Measures, weights, and lipid levels in migrating Dunlins *Calidris a. alpina* L. at the Ottenby Bird Observatory, South Sweden

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Measurements, weights, and lipid levels of 85 Dunlins collected during two autumn seasons at the Ottenby Bird Observatory in South Sweden were analyzed. Males had significantly shorter wings and bills, and lower body weights than females. Fat depots ranged from about 5 to 30 per cent of total weight and accounted for the major variations in body weight. No correlation was found between body size and lipid level. The water content expressed as a percentage of fat-free weight was virtually constant within each year sample, irrespective of body size and lipid level. Significant differences in fat-free dry weights and water content between the two year samples were found. A formula for calculation of fat stores from total weight and wing length is presented. The results are compared to other work on waders and passerines.

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Introduction

In contrast to the comprehensive information available on seasonal weight variations and migratory fat accumulation in passerines, data on limicoline species are scarce. The Dunlin *Calidris alpina* is among the few waders previously studied. Fuchs (1973) investigated total weight variations and fat classes in palaeartic Dunlins *C. a. alpina* and *schinzii* resting in the Camargue, southern France. Total weight variations in summer and winter populations of the North American Dunlin *C. a. pacifica* were analyzed by Holmes (1966), and Yarbrough (1970) studied summer lipid levels in the same subspecies.

In an earlier investigation on the palaeartic subspecies *C. a. alpina* at the Ledsjär Bird Observatory in Middle Sweden, Mascher (1966) roughly calculated fat-free weights and lipid levels from field data on total weights and wing lengths. As laboratory analyses were unavailable at that time, the estimates of fat depots were made on the assumptions that fat deposition is responsible for the major variations in total weights

allowing for body size, that wing length is a good estimator of body size, and that the lowest total weights observed were roughly equal to the fat-free weight.

To study the fat deposition in migrating Dunlins more thoroughly an investigation was carried out at the Ottenby Bird Observatory in South Sweden which included freeze-drying and fat extractions of collected specimens. This paper presents data on wing and bill lengths as well as total weights, dry weights, water content, and fat accumulation in a sample of 85 Dunlins caught during migrations at Ottenby in two consecutive autumn seasons 1969–70. An analysis of the relations between wing length and various body components is made.

Material and methods

In cooperation with the personnel at the Ottenby Bird Observatory, Dunlins were caught in net cages on the shores at the southernmost point

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Table I. Wing and bill lengths in Dunlins collected at Ottenby in 1969 and 1970. The figures indicate mean (m), range and standard error (S.E.) of mean. Two specimens in 1969 were unsexed

Year	n	Wing length (mm)			Bill (mm)		
		m	range	S.E.	m	range	S.E.
1969	♂	8	115.6	(113–120)	0.85	29.9	(27–33)
	♀	10	118.3	(115–120)	0.49	33.9	(32–37)
	all	20	117.3	(113–120)	0.52	32.2	(27–37)
1970	♂	38	116.4	(113–121)	0.38	31.5	(28–37)
	♀	23	119.4	(111–122)	0.58	34.8	(32–37)
	all	61	117.2	(111–122)	0.35	32.8	(28–37)

of Öland. They were measured, weighed, killed with ether, and immediately frozen. In the first autumn only 20 birds could be obtained because Dunlin migration failed almost totally at Ottenby that year. 65 additional specimens were collected in 1970. In 1969, birds were taken on September 22nd (16), 24th (1), 26th (1) and on October 14th (2). In 1970 the collections were made somewhat earlier, on the 7th (58), 9th (2) and 18th (5) of September. With one exception, all birds were juveniles.

Wing and bill lengths as well as total weights were measured on all birds in the laboratory after they had been kept frozen for about one year. The analyses presented are based on these data, with the exception of wing lengths for 1969 taken on the living birds. The reason for using the laboratory data is that only a few birds were actually measured alive at Ottenby. A comparison with measures taken on some birds before they were killed does not show any significant discrepancy.

The analyses of dry weights and fat content of the collected birds were performed at the Institute of Zoophysiology, Uppsala. The liver was taken out of the body and analyzed separately. The dry weight was determined by grinding the specimens to a thick mixture that was freeze-dried to constant weight. The lipid analyses were carried out according to Soxhlet with a mixture of 1 part ethanol and 3 parts ether. Because of the presence of alcohol, not only free lipids but also part of the lipo-protein complexes were included in the extract. After the complete vaporization of ether and alcohol, the quantity of extracted lipid was weighed.

Statistical analyses including correlation coefficients, regression coefficients, and t-values to

test the significance of correlations were performed with the aid of ADB equipment at the Institute of Technology, Uppsala.

The terminology used for different weight fractions is as follows:

Total weight = weight of the intact body. Dry weight = total weight minus water. Fat-free weight = total weight minus fat. Fat-free dry weight = total weight minus fat and water. Fat content or lipid level = amount of ether-ethanol extracted material. Water content = total weight minus dry weight.

Results

Wing and bill lengths

Bill lengths were slightly but significantly shorter in 1969 than in 1970, but there were no significant differences in wing lengths between the two years (Table I). Males had significantly shorter wings and bills than females, though there is a considerable overlap.

According to the measurements, the birds studied clearly represented the *alpina* subspecies in both years. The data conform well with earlier material from Ottenby (Martin-Löf 1958, cf. Soikkeli 1966) and Ledskär (Mascher 1966 and unpubl.).

There was a highly significant positive correlation between wing and bill lengths, as was to be expected (correlation coefficients 0.54 in 1969 and 0.49 in 1970; $p < 0.01$ and $p < 0.0005$, respectively). As is shown later, bill length is almost as good an estimator of fat-free dry weight as is wing length.

Table II. Total weights and body components in Dunlins collected at Ottenby in 1969 and 1970. Number of specimen 20 (8 ♂, 10 ♀, 2 unsexed) in 1969, 65 (38 ♂, 27 ♀) in 1970. All values in g where not otherwise stated. Figures indicate mean, range, and standard error of mean

		1969			1970		
Total weight	♂	42.9	(38.7–47.9)	1.2	48.7	(37.8–59.2)	1.0
	♀	49.6	(40.5–65.2)	2.4	51.2	(40.2–67.7)	1.4
	all	46.6	(38.7–65.2)	1.5	49.7	(37.8–67.7)	0.9
Fat-free weight		40.8	(32.4–47.4)	0.9	42.1	(35.7–50.3)	0.4
Fat-free dry weight	♂	9.4	(8.9–9.9)	0.2	12.7	(11.3–15.8)	0.2
	♀	10.4	(9.3–11.8)	0.3	13.6	(11.4–15.4)	0.2
	all	10.2	(8.9–13.4)	0.3	13.1	(11.3–15.8)	0.1
Fat, weight		5.8	(2.3–19.0)	0.9	7.7	(2.0–19.6)	0.5
Fat, % of dry weight		33.5	(19.5–63.8)	2.7	34.4	(14.3–57.3)	1.5
Fat, % of total weight		11.9	(5.6–29.2)	1.3	14.7	(5.0–29.2)	0.8
Water, weight		30.7	(22.5–35.6)	0.8	29.0	(24.3–35.6)	0.3
Water, % of fat-free weight		75.0	(69.3–78.4)	0.5	69.0	(67.4–71.1)	0.1
Liver, total weight		2.4	(1.7–3.5)	0.1	2.7	(1.5–3.8)	0.1
Liver, % fat of dry weight		11.5	(9.4–16.2)	0.5	17.4	(4.5–26.9)	0.5

Total weights

Total weights and body components of the collected Dunlins are presented in Table II. Total weights averaged about 4 g higher in the 1969 birds when they were weighed alive compared with the data obtained at the laboratory. This was not the case concerning some birds weighed both alive and dead in 1970. Little seems to be known about the possible weight loss which may occur in animal bodies kept frozen. Banks (1965) found a slight weight decrease of 0.35 per cent in small mammals after three months freezing. Even after a year-long period of freezing, weight loss in frozen birds kept in closed plastic bags should be negligible for the purpose of the present study. To avoid a possible bias from methodological errors in the weighing of living birds during the two years, only the uniform weight data from the laboratory are used in the analyses presented below.

Total weights of birds collected in 1969 were significantly lower than those collected in 1970 (Table II). The difference is most pronounced in the males. 502 juvenile birds caught at Ledsjär in September 1963 (Mascher op. cit.) averaged 44.2 g (standard error of mean=1.0), which is lower than the data from Ottenby. This difference is within the range of weight variations caused by normal fluctuations in fat stores in migrating birds; for a closer interpretation laboratory analyses of dry weights and fat content are needed.

Liver weight and fat

There were very small variations in wet and dry liver weights, unimportant considering the data on the whole body. Statistical analyses showed strong positive correlations between total liver weights and body minus liver as well as between fat accumulation in the liver and the rest of the body. The fat content of the liver is small but the general accumulation of migratory fat is reflected also in the liver (Fig. 1).

The percentage of liver fat was significantly higher in 1970, which is in accordance with somewhat larger body fat stores that year. For the purpose of further analyses it was considered justifiable to add the liver data to the rest of the body.

Fat content

As is clear from Table II, fat depots were larger in 1970, on the average, than in 1969. Individual variation in fat content is considerable, as is usual in a population of resting migrants which have been travelling different distances and resting for different periods before they were caught. Presumably, the lowest recorded values of 5–6 per cent fat of total body weight are near a non-migratory level in birds without stores of migratory fat. Very similar figures are indicated by the data published by Yarbrough (op.cit.) on specimens of *C. a. pacifica* collected on their breeding grounds in Manitoba. It has been shown

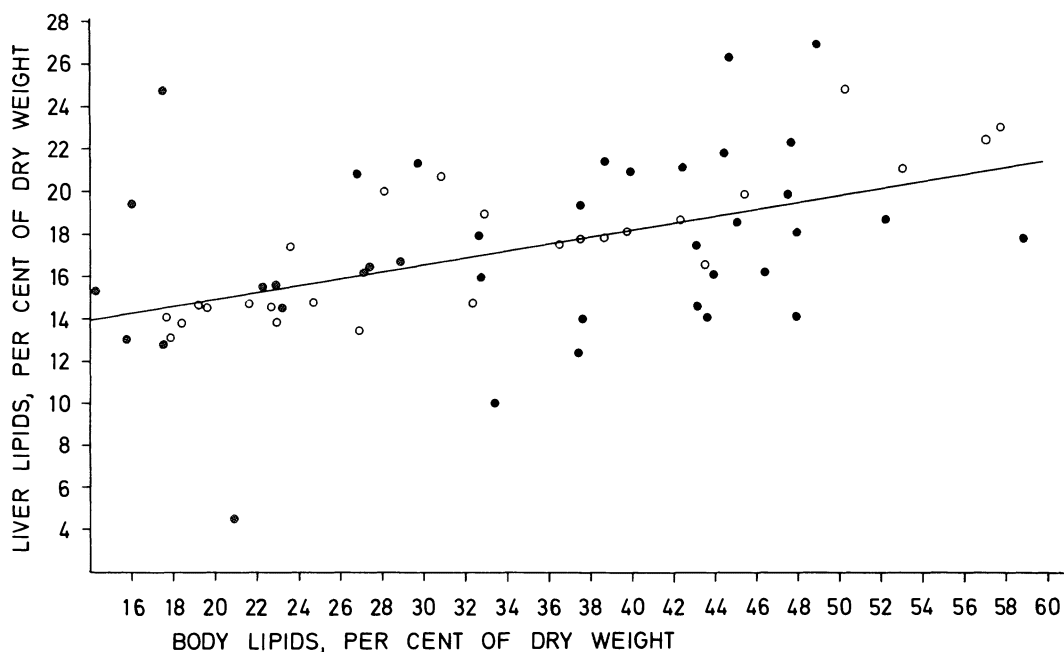


Fig. 1. Relation between lipids in body minus liver, and in liver, expressed as a percentage of dry weight. Correlation coefficient (r) = 0.54. Regression coefficient (b) = 5.9. Level of significance (p) < 0.0005. Regression line computed according to the formula $y - \bar{y} = b(x - \bar{x})$. ● = males, ○ = females.

by Odum (1960), Ward (1964), Johnston (1966) and others, that the average fat content in non-migratory passerine species ranges roughly between 4–6 per cent.

Mean levels of fat in the two years amounted to 11.9 and 14.7 per cent respectively, and the maximal fat accumulation recorded was 29.2 per cent of total weight in both years. The fattest bird had about 10 times more lipids than the leanest specimen.

Earlier data on Dunlin fat accumulation in the same subspecies at Ledskär, Middle Sweden (Mascher *op. cit.*) were based on rough estimations of fat-free weights which were subtracted from total weights. The present analyses indicate that the fat-free weights were calculated about 5–6 g too low in the Ledskär birds, and the figures on their fat content should be reduced accordingly. However, caution is warranted because of the constitutional differences which may occur between populations (*cf.* p. 53). If the data on fat-free weights in the Ottenby birds are applicable to the populations which were studied at Ledskär, fat deposition in the latter group averaged 12–13 per cent, which conforms well to the Ottenby figures presented here.

Fuchs (1973) calculated fat depots from total weights in Dunlins mainly of the nominate subspecies resting in the Camargue. If the present results on fat-free weights are applicable to the populations studied by him, his figures on fat content should be reduced about 4 g resulting in average monthly fat proportions between 10 and 16 per cent of total weight with a maximum in November. His highest fat value in the autumn amounts to 32 per cent but in spring there were records of 40 and 42 per cent in extreme cases. The figures are in good conformance with the present material and as Fuchs points out, it is clear that the migrating Dunlin contingents still have appreciable fat reserves when they reach the Camargue.

An interpretation of Yarbrough's (*op. cit.*) figures indicates that the mean fat proportion of total body weight was about 20 per cent in North American Dunlins arriving at the breeding grounds in Manitoba. The comprehensive material on total weights in this subspecies on summer and winter grounds collected by Holmes (*op. cit.*) indicates a mean pre-migratory fat accumulation of a similar magnitude. Clearly, much larger fat stores occur in individual cases.

The data available on both Dunlin subspecies concerning the magnitude of fat accumulation are not quite comparable as the American subspecies was not actually studied during the course of the passage. In passerine species maximal fat stores of 30–50 per cent of total weight are by no means exceptional (Odum 1958, 1960, Nisbeth et al. 1963, and others).

It should be stressed that the results of different workers must be compared with great caution, considering certain differences in the extraction methods which may account for differences in lipid levels, fat-free dry weights, water etc.

Fat-free weights

Fat-free weights averaged 40.8 g in 1969 and 42.1 g in 1970 (Table II). In the Ledsjär study earlier referred to (Mascher op. cit.), fat-free weights were roughly calculated from the observed variation in total weight and the lowest noted weights which were presumed to be near the fat-free level. As already mentioned, the estimate of about 34–35 g fat-free weight in the Ledsjär birds is probably about 5–6 g too low.

Fuchs (op.cit.) studied total weights in the same subspecies in the Camargue and estimated a mean fat-free weight of 37 g. According to the present results, this figure is about 4 g too low, if the same populations are concerned.

Fat-free dry weights are lower compared with Yarbrough's data on *C. a. pacifica*, which should be expected since the nominate subspecies is of smaller size. A comparison of the two samples from Ottenby in 1969 and 1970 shows that the 1969 sample averaged 3 g lower. The difference is significant. One specimen in 1969 had an aberrantly high fat-free dry weight near the mean of the 1970 sample. In addition, its water content was aberrant (cf. below).

Water content

The water content expressed as a percentage of fat-free wet weight was significantly higher in 1969. Within each year sample, the proportion of water in the fat-free body mass was remarkably constant and uncorrelated to fat deposition (Fig. 5). Three specimens in 1969 had considerably lower percentages of water, conforming closely to the 1970 group (Fig. 6).

Discussion

Fat-free weights and water content

A methodological bias as an explanation of the differences in fat-free dry weights and water content between the two year groups seems ruled out by the fact that five birds – which did not include the three specimens with lower water content – from the group collected in 1969 were analyzed together with the 1970 group but still conformed to the earlier analyses. The extractions were performed in exactly the same manner both years. Although each year-sample was analyzed in smaller parts during the course of several months, the data within each year-group are in close conformity.

Further, it seems difficult to explain the significant differences in fat-free dry weights and water content between the two year-samples in physiological terms. The small range of variation in these variables each year is in accordance with many studies on passerines, e.g. by Odum et al. (1964), Hicks (1967), Child (1969), and Child & Marshall (1970), which have shown that non-fat dry body mass and water content were remarkably constant irrespective of age, sex, size, fat accumulation etc. while the major variations in total weight were caused by variations in fat stores.

However, some contradictory studies in recent years have revealed substantial fluctuations in both water and fat-free dry weight correlated or uncorrelated to changes in lipid levels (Fry et al. 1970, Moreau & Dolp 1970, Dowsett & Fry 1971, Fogden 1972, and others). Evans (1969) and Fry et al. (op. cit.) claim that a premigratory increase in fat-free dry weight which accompanies fat accumulation may reflect an increase in flight muscle mass as an adaptation to migration. According to Dowsett & Fry (op. cit.), the non-fat tissue hypertrophy may amount to 10 per cent of premigratory weight. As concerns the present material of Dunlins, the data were collected during the migratory phase when flight muscles already should be maximally developed.

Concerning water content in migrating birds, some workers (e.g. Yapp 1956, Moreau & Dolp op. cit., Fogden op. cit.) state that a dehydration takes place setting a limit for the range of a migratory flight. The Dunlins analyzed were collected from resting populations which probably had replenished their water losses. In passerines, low fat-free weights and water contents have been recorded after exhausting flights over open water, when they had depleted their

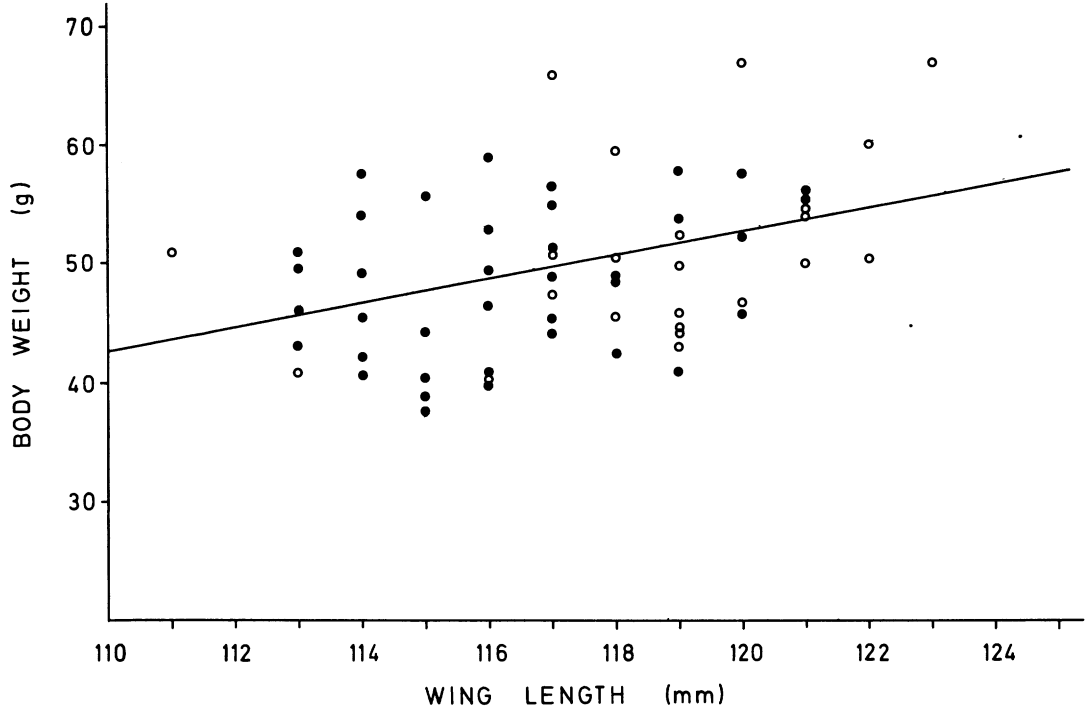


Fig. 2. Relation between wing length and total weight. $r = 0.40$, $b = 1.03$, $p < 0.0025$.

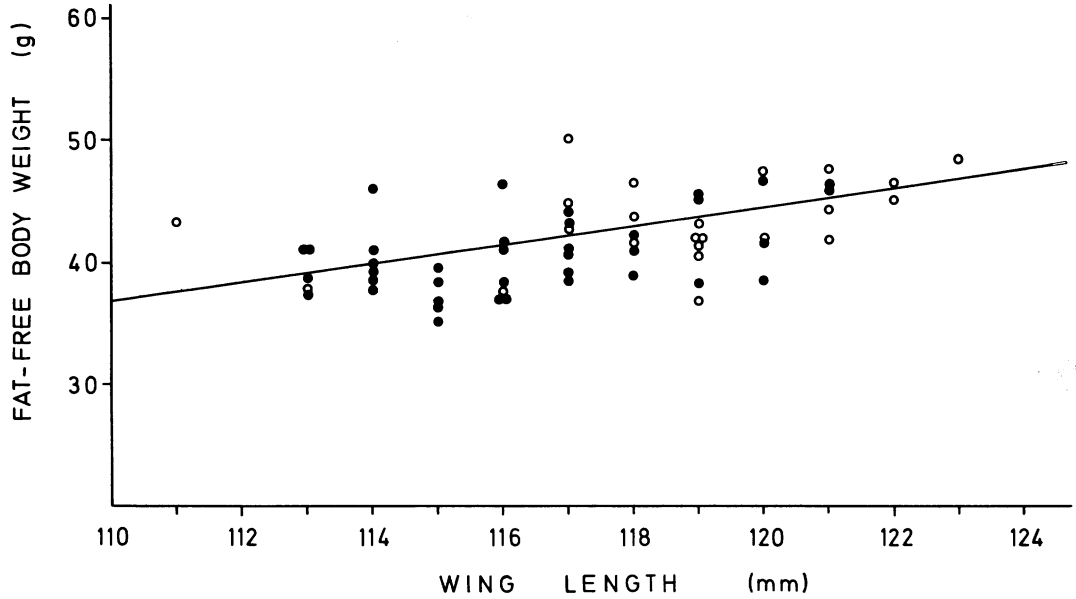


Fig. 3. Relation between wing length and fat-free weight. $r = 0.53$, $b = 0.69$, $p < 0.0005$.

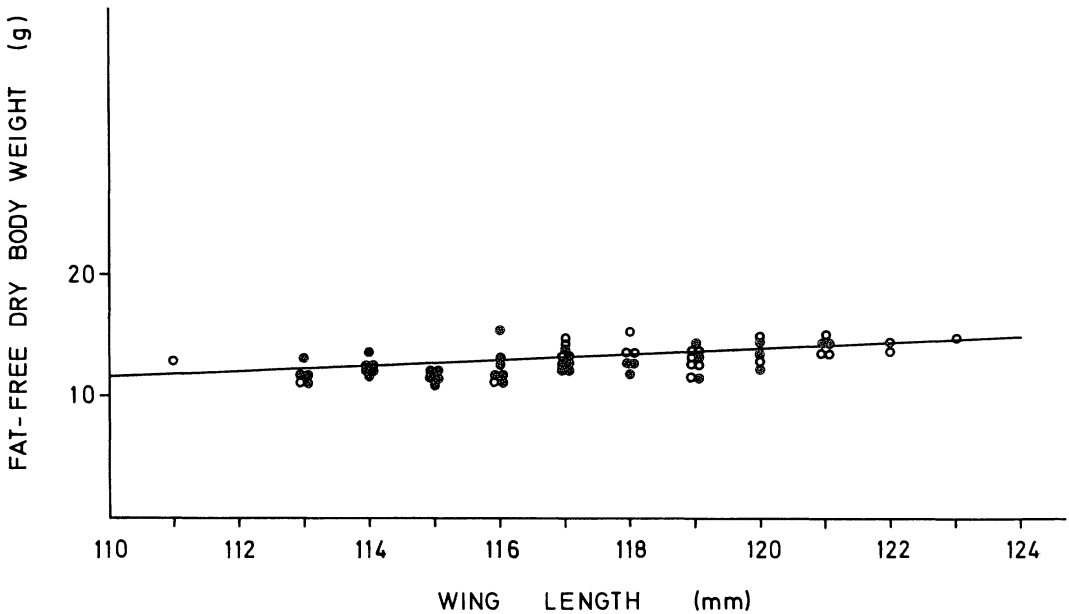


Fig. 4. Relation between wing length and fat-free dry weight. $r = 0.59$, $b = 0.24$, $p < 0.0005$.

fat stores and presumably were using part of their fat-free tissues as fuel (Voous 1957, Nisbeth et al. op. cit., Rogers & Odum 1966, Johnston 1968). Shore-birds travelling along the coasts of Scandinavia would hardly be exposed to such a stress.

Thus, although the concept of homeostasis of non-fat tissues in migrating birds is perhaps not as generally valid as stated by Odum et al. (op. cit.), it may be applicable to a homogeneous resting population in the migratory period. This assumption is supported by the present data on resting Dunlins at Ottenby.

The possibility should be considered that the general difference in fat-free dry weights and water content between the two years was on a populational level and that the three aberrant birds with lower water content in 1969 represented the same population as was collected in 1970. Though the usual measurements taken in the field were identical, other constitutional differences between populations might well occur, considering the vast area from which the *Calidris a. alpina* contingents migrating past the Swedish shores are recruited: from northern Scandinavia through the northern Soviet Union to Taimyr and perhaps further east. Slightly larger measurements have been recorded in individuals in the eastern part of this range of distribution and

a further subspecification has been claimed (*Calidris alpina centralis* Buturlin). The larger subspecies *C. a. sakhalina* is not known for certain to occur in Sweden, but contingents of birds which seem generally to be of larger body size have been noted (Martin-Löf 1958, Mascher op. cit.). Differences in other variables and measurements may occur as well.

Correlations between wing length and weights

Males and females were not separated in the statistical computations of regressions and correlations; this seems warranted because there is no indication of principal discrepancies between sexes concerning the relations between measurements and different body components. The uniform distribution of data with males at the lower and females at the upper end of the regression lines apparently only reflects a size difference as displayed in measurements and weights.

With one exception, only the data from 1970 are presented in the correlation diagrams as the picture was generally the same in the much smaller 1969 group.

As is already evident from the analyses of fat, fat-free dry weight, and water content, fat accumulation is responsible for the major variation in total weight. The picture is clear from the

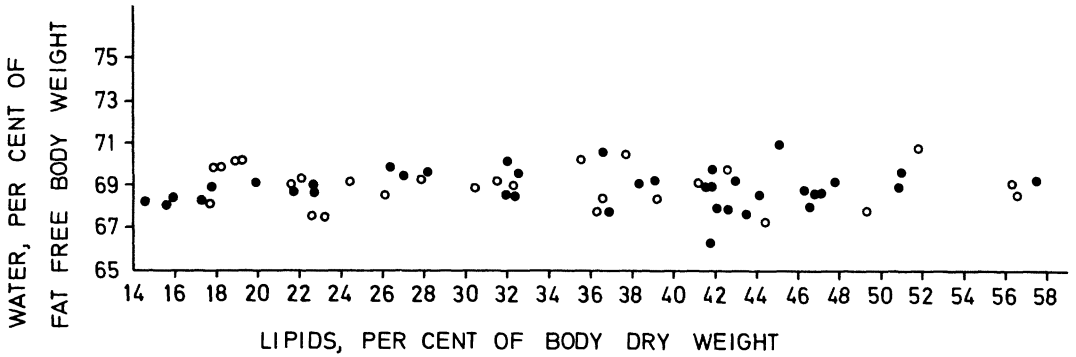


Fig. 5. Lipids as a percentage of dry weight compared to water as a percentage of fat-free weight. The variables are uncorrelated.

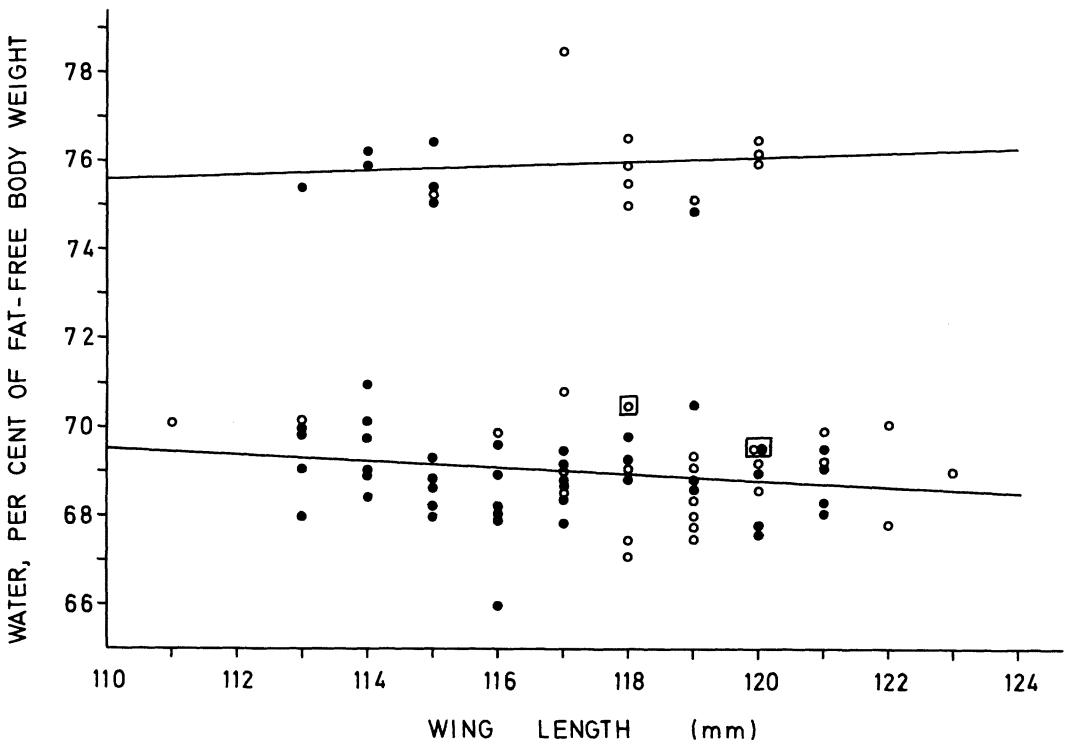


Fig. 6. Relation between wing length and water as a percentage of fat-free weight. The regressions are barely significant. 1969 (top): $r = 0.35$, $b = 0.05$, $p < 0.1$. 1970 (bottom): $r = -0.22$, $b = -0.07$, $p < 0.05$. The diagram illustrates the differences in proportional water content between the two year samples. Three specimens in 1969 which conformed with the 1970 sample are marked \square . They were excluded from the statistical computations.

regression diagrams Fig. 2–4. Although the correlation between wing length and total weight is highly significant, the range of variation is considerable within each wing-length group. When fat is excluded, the variation is substantially

smaller, and when both water and fat are subtracted, the remaining fat-free dry weights vary only about 2–3 g in each group. The variations in fat-free dry weights mainly depend on differences in body size (Fig. 4). However, the total

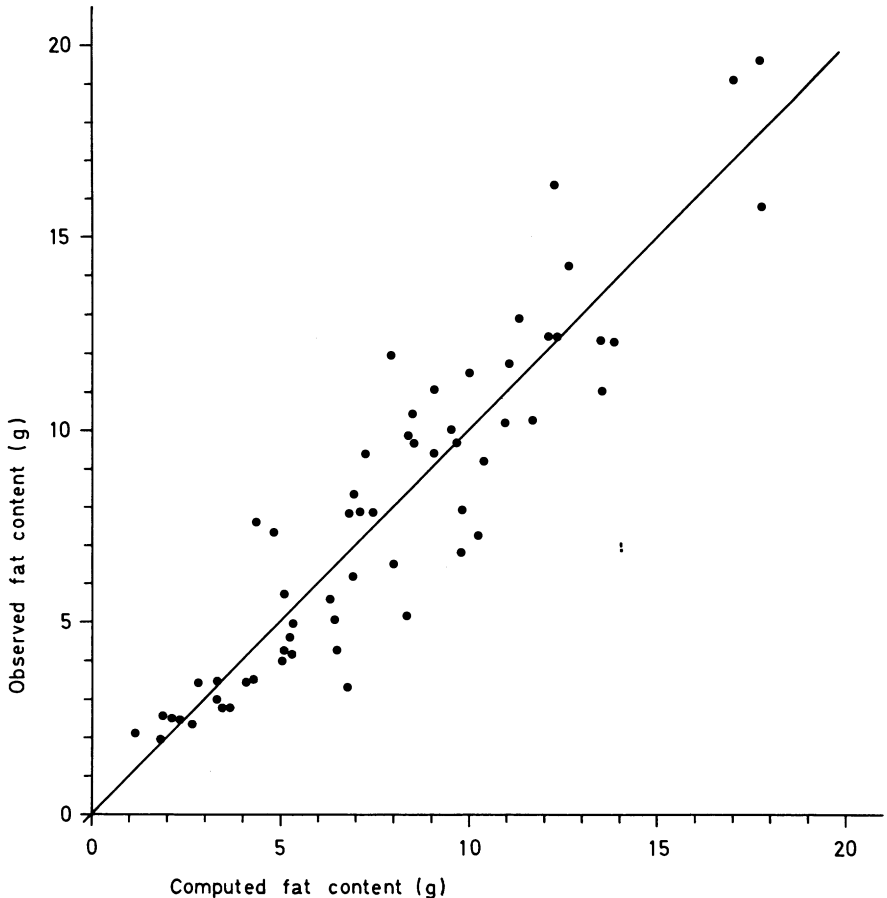


Fig. 7. Observed fat content compared to figures plotted from the formula: fat content = $10.84 + 0.61 \times \text{total weight} - 0.28 \times \text{wing length}$ which was computed by bivariate regression using the data from 1970 (cf. text). Parameters were chosen to minimize the standard error of the deviation from actual values. The standard error = 1.67. The error of the computed fat content is within ± 3.3 g in 95 per cent of the cases.

range of variation is small, and there is a gain of not more than 0.24 g fat-free dry substance for each mm of increasing wing length. These results invalidate the earlier estimation from total weight–wing-length relations in adult and juvenile Dunlins (Mascher op. cit.) of a weight gain of 0.41 g (ad.) and 0.59 g (juv.) per mm wing length and show that laboratory analyses are essential for such calculations.

For comparison, bill lengths were also correlated to fat-free dry weights in the 1970 group. Very similar correlation (0.54) and regression (0.28) values were obtained (cf. Fig. 4). The level of significance was also high, but somewhat lower than that of the wing length–fat-free dry weight regression.

The strong correlation between wing length and fat-free dry weight in the Dunlins is in accordance with the classical studies on passerines by American workers, e.g. Connell et al. (1960). Rogers & Odum (1964) claimed that they could predict fat-free wet weights from wing lengths in wood warblers (*Dendroica* sp.) with an accuracy of 4 per cent. Data on limicoline species are scarce, but Pearson & Phillips (1970) found good correlations between wing lengths and total weights in wintering waders in Kenya, although they did not analyze fat content and fat-free weights.

On the other hand there are contradictory results, e.g. by Moreau & Dolp (op. cit.) and Snow & Snow (1963). These authors found no or

very weak correlations between wing length and fat-free dry weights in passerines. Concerning the work by Moreau & Dolp on spring migrants in North Africa, the possibility should be taken into account that different populations with different geographical origin were represented in the samples studied.

In the present Dunlin material there is a highly significant positive correlation between wing length and water content which mainly reflects differences in body size. A slightly larger proportion of water was found in the smallest birds of 1970, but the correlation is barely significant (Fig. 6). A comparison of water content as a percentage of fat-free body weight and fat supply as a percentage of dry weight reveals that even large variations in fat accumulation are not correlated to changes in the water component of the body (Fig. 5).

Some authors have attempted to construct equations for calculation of fat stores from different variables. Child & Marshall (op. cit.) showed that the fat content of passerine migrants could be fairly accurately predicted from the water content because of the constancy of the latter and the fat-free dry weight irrespective of the magnitude of fat stores. This method presupposes laboratory analyses of the birds studied. McNeil (1969) assessed lipid levels in several limicolines from a visual classification of subcutaneous fat deposits which showed good agreement with laboratory analyses of fat content. However, there is a considerable amount of subjectivity connected with the visual or tactile estimation of fat classes.

For the purpose of field studies on migrants it would be an advantage if the fat content in living birds could be estimated with reasonable accuracy from total weights and wing lengths, i.e. properties easily measured in the field. This would be possible if laboratory analyses on a relevant sample of birds showed small variations in proportional water content and a strong correlation between wing length and fat-free dry weight.

In the present material of Dunlins, the variations of each of these variables, i.e. water content and fat-free dry weight, are relatively small, but the added effect of them is considerable (cf. Fig. 3). The range of variation within each wing length category (mm) amounts to about ± 5 g. With the aid of bivariate regression analysis, the following formula for estimating fat content from total weight and wing length has been computed using the 1970 data:

$F = 10.84 + 0.61TW - 0.28WL$, where F is amount of fat in g, TW total weight in g, and WL wing length in mm.

The variables were chosen to minimize the standard deviation of the error. A good correlation with the actual fat extractions is obtained as shown in Fig. 7. The error is reduced to within ± 3.3 g in 95 per cent of the cases by a standard deviation of 1.67 g. The formula presented yields reasonably accurate estimates of the fat content in living birds and should be applicable to larger samples of birds to classify fat levels if the population studied is homogenous. The data from 1969 and 1970 indicate that this may not be the case concerning Dunlins on passage at Ottenby, presumably because of some variation in proportional body components within the subspecies. This point needs further elucidation.

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