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WEIGHT VARIATIONS IN RESTING DUNLINS (*CALIDRIS A. ALPINA*) ON AUTUMN MIGRATION IN SWEDEN

(Ledskär Bird Station Report No. 5)

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INTRODUCTION

The ability of many migratory birds to deposit large amounts of fat prior to their spring and fall movements has been a well-known fact since the early 19th century (Naumann 1822, Wachs 1926, Zeidlitz 1926, Groebbels 1928, 1932, Linsdale & Sumner 1934 a, b, Merkel 1937, 1938, Baumgartner 1938, Blanchard 1941, de Bont 1947, Blanchard & Erickson 1949, Odum 1949, Steinbacher 1951, Schüz 1952, Schildmacher & Steubing 1952, Weise 1956, Curry-Lindahl 1958, 1963 a, b, King & Farner 1959, Helms 1959, Helms & Drury 1960, Dolnik 1963, etc.). Odum (1958), Drury & Keith (1963) and others have shown that the premigratory fat storage, acting as a source of muscle energy for long non-stop flights, can amount to proportions as high as 40-50 per cent or even more of the total body weight in certain passerine species. These reserves of energy may be almost completely used up as a result of sustained migratory activity, but are rapidly replenished under resting conditions (Bryson 1951, Williamson 1952, 1955, Voous 1957, Davis 1962, Rogers & Williamson 1963 and others).

The first quantitative measurements of body lipids in migratory birds were performed by Odum & Perkinson (1951) working with populations of White-throated Sparrows (*Zonotrichia albicollis*) on their wintering grounds. As a matter of fact, the fat-free weight, as determined by extractions of samples of collected specimens, is remarkably constant in birds of the same species and size (wing-length). Thus, the spectacular changes in weight occurring before, during and after the migratory period depend primarily on variations in fat reserves (cf. also Farner, Mewaldt & King 1954, King & Farner 1959). The amount of body fat as an indicator of the migratory state of resting birds can be accurately calculated from the total live weight by subtracting the corresponding fat-free weight as an earlier computed constant (Connell, Odum & Kale 1960).

A lot of evidence has been collected in this field of study in recent years, which has thrown light upon the phenomenon of fat accumulation in migratory birds as a physiological adaptation necessary for the performance of long-range flights (reviews in Wolfson 1945, 1954 a, b, Farner 1955, 1960, Rautenberg 1957, Lack 1960,

TABLE 1. RINGING FIGURES AND RESTING-TIMES AS RECORDED FROM TRAPPINGS AND RETRAPPINGS OF DUNLINS ON AUTUMN PASSAGE AT LEDSKÄR. (ALL BIRDS OF UNKNOWN AGE WERE EXCLUDED FROM THE COMPUTATIONS, AS WELL AS 41 BIRDS RINGED IN OCTOBER 1962, WHEN NO CONTINUOUS TRAPPING WAS PERFORMED).

Resting-times, days after ringing	Recaptured birds																				Ringed, total		unknown age				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22		Total	Per cent of total ringed	ad.-juv.	
1962										1						1							28	45,9	61+(41)	20	
	juv.	7	4	5	4	5	1																				
	ad.	11	5	4	1	1	3	1	3	1							1						31	18,0	172		
1963																								197	672	44	
	juv.	53	24	23	15	14	12	11	9	11	3	6	5	5	2	1	1						1	29,3	672		
	ad.	15	6	9	1	1																	32	14,5	220		

Dolnik 1961, Dorst 1962, West 1962, King & Farner 1963, Schildmacher 1963). The important implications of the collected data for the possible flight ranges of smaller birds have been discussed by several authors (Yapp 1956, 1962, Williamson 1958, Lack 1959, Odum 1960 a, Odum, Connell & Stoddard 1961, Moreau 1961, Drury & Keith 1963, Graber & Graber 1962, Nisbet, Drury & Baird 1963, Schildmacher 1963, Eliassen 1963, Pearson 1964). However, almost all research so far has concerned itself with smaller passerine birds. The purpose of this paper is to present some field weight data on Dunlin (*Calidris a. alpina*) populations on autumn migration through southern Scandinavia, and to compare the results with those of earlier investigations on passerines.

THE INVESTIGATION AREA

The investigation was performed at the Ledskär Bird Station, situated at the Lövsta Bay of the southern Bothnian Sea, province of Uppland (60° 30' N; 17° 43' E). The innermost part of the Lövsta Bay is characterized by open shores with wide grass-meadows and sandy banks bordering the very shallow water, thus offering attractive resting-places for migrating waders of many species. In these respects the locality is fairly unique for this part of Sweden (Norling, Pettersson & Ståhl 1956, Fredga & Frycklund 1965). In addition, swarms of waders and other shore-birds moving southwards along the Bothnian coast or crossing the sea from Finland are presumed to be "caught up" in this deep bay where the coastline diverges sharply from their migratory route. As a consequence many of them may interrupt their journey and rest on the shore for a while before taking course southwards again, now being forced inland.

Thus the local conditions are very favourable for the performance of field observations including ringing activity, and the Ledskär Bird Station has been working on this spot since 1956 (Lundin & Pettersson 1959, Frycklund 1964, Norlin 1965). A ringing program of waders, mainly trapped in net-cages on the shore, has been carried on since 1957 (Fredga & Frycklund (1965). Because of the concentration of resting waders within a fairly restricted area, comparatively high proportions of recaptures are obtained. Thus the conditions are especially convenient for studies on weight variations of resting birds during the time they spend on the shore before departing.

MATERIAL AND METHODS

The investigation was initiated in 1962 and continued through 1963. The total ringing figures and recaptures of adults and juveniles during the two seasons are shown in Table 1.

In 1962, the bird station was manned continuously between June 15th and August 31st, from then on only occasionally. Mainly on account of this short period of work, only 294 Dunlins were ringed that year, comprising 172 adults (yielding in all 43 recaptures), 102 juveniles (48 recaptures) and 20 unclassified. As this material was considered insufficient for the purpose of weight analysis, it is only briefly referred to in the following discussions. The collected weights

and measures generally showed good conformity with those of the next season, with the notable exception of some divergent data on the juveniles obtained in October, to be discussed later.

In 1963, the ringing work ended on September 29th. During October, when occasional visits were paid to the station, no trapping work was possible because of high water flooding the banks. Through out the season 936 Dunlins were trapped, comprising 220 adults (42 recaptures), 672 juveniles (333 recaptures) and 44 of unclassified age. Many of these birds were caught several times during their stay on the shore. Some were retaken on up to 6-7 different days. Not uncommonly the same bird was retrapped on two—and in a few cases even on three—occasions on one day.

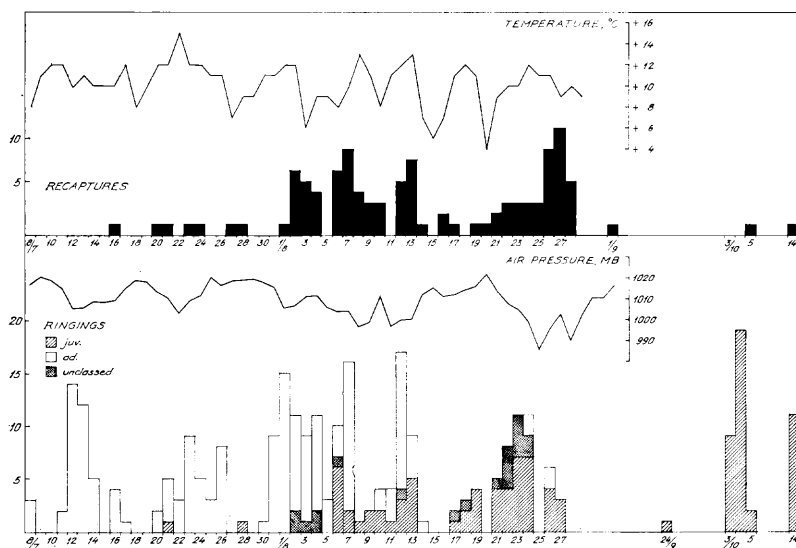
In the following discussions on weight variations the data on the juveniles obtained in 1963 are primarily considered, as they comprise a material large and unitary enough to justify a more elaborate statistical treatment. It was considered unwise to lump together the two-year material since the possibility of inherent incongruences (e.g. the occurrence of different populations) causing distortion of the results could not be ruled out. However, one exception to this was made. In computing the weight—wing length relation of the adults, the two-year material was added together, as the distribution of weights and measures from the two seasons were in quite close conformity. All birds of unclassified age were excluded from the computations.

As part of the routine ringing work, measures and weights were taken of all Dunlins trapped. All recaptures were also weighed. The birds were mainly caught in net-cages arranged in groups or series on the shore and connected through strips of net. Fredga & Frycklund (1965) have described the construction of these traps. The traps were cleared about once every hour, and the birds were immediately carried to the bird station, where all manipulations took place. A minor proportions of birds were caught at night in Japanese mist nets. On an average, the birds were detained for about $\frac{1}{4}$ - 1 hour after entering the traps or nets until they were weighed. They were released after about an additional $\frac{1}{2}$ hour. As is clear from the proportions of recaptures, the trapping effectiveness at times exceeded 60 per cent (cf. Figure 10) though it was obviously greatly influenced by variations in water level, weather conditions, etc.

During the first season the birds were weighed on a two-lever balance accurate to 1/10 gm. In the following year, all weighings were performed with a spring balance purchased from the British Trust for Ornithology, which was accurate to $\frac{1}{2}$ gm. The calibrations of the two balances were in exact conformity as was clear from a series of control weighings on both. All weights were later levelled to the nearest 1 gm, as a preliminary analysis revealed that the smaller variations had no relevance to the main changes of diurnal or daily weight in a species of this size.

Wing lengths were measured with the wing flattened. The accuracy was within 1 mm. These and other measures taken on total length, bill and tarsus will be more exhaustively accounted for in a later publication and are not analysed in detail here.

Fig. 1. Daily ringing (lower) and recapture (upper) numbers of Dunlins at the Ledskär Bird Station in 1962. Lower curve: Barometric pressure at 0700. Upper curve: Minimum temperature during the preceding night.



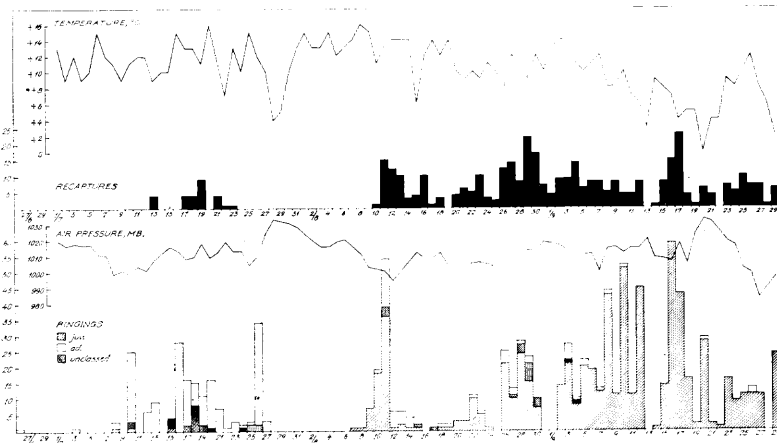
To facilitate the later analysis of the data, all measures and weights were collected on numbered charts, one for each bird according to ring-numbers. In particular, this system rendered the task of registering the recapture weights very easy.

THE GENERAL COURSE OF DUNLIN MIGRATION AT LEDSKÄR

The Dunlin is quite outstanding in number among the *Calidris* species migrating through the Baltic Sea area. Apparently, the populations occurring on autumn migration in southern Sweden almost exclusively belong to the subspecies *C. a. alpina*, which breeds in Scandinavia east to Yenisei (Witherby *et al.* 1949). It is not clear to what an extent the form *centralis* maintained by some authors (e.g. Gladkov 1951, Portenko *et al.* 1953) and ranging roughly from Yenisei to Lena may migrate through Scandinavia. No certain records of the larger *C. a. sakhalina* breeding in E. Asia have been reported in Sweden. The range of *C. a. schinzii* in south Sweden extends north to Uppland; 1-3 pairs yearly breed at Ledskär and a few specimens may have been included in the earliest captures of the season. However, in comparison with the large numbers of migrating birds of the nominate race, they are by far too few to cause a serious bias in the results of the present investigation.

The Dunlins occur regularly on autumn migration at Ledskär from the first week of July until early (or in certain years, the middle of) October. During July and early August the adult population

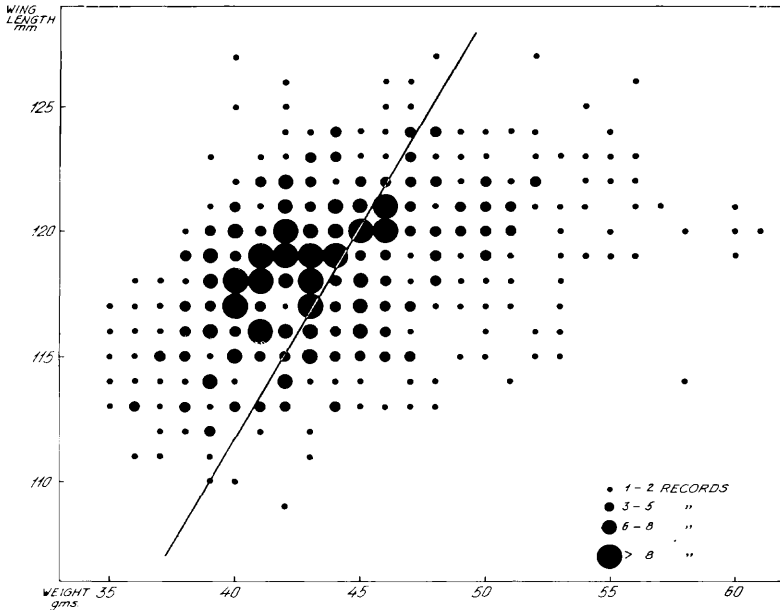
Fig. 2. Daily ringing (lower) and recapture (upper) numbers of Dunlins at the Ledskär Bird Station in 1963. Lower curve: Barometric pressure at 0700. Upper curve: Minimum temperature during the preceding night.



forms the bulk of the resting flocks. Usually, the juveniles begin to arrive about the first week of August and then dominate in number from the middle of this month. After this date few adults are usually seen. In certain years, however, there is a distinct gap of one week or more between the disappearance of the adult and arrival of the juvenile contingents. This was the case in 1963, when there was a pause in the passage, amounting to 10 days. Though the resting swarms by no means are comparable in size to those locally occurring in south Sweden, they sometimes attain numbers of several hundred individuals during the peak of the migratory period in August and September.

Figures 1 and 2 show the course of Dunlin migration during the two years of investigation as reflected in daily ringing figures and recaptures. The passage is obviously much faster early in the season than later. In July, when the adults dominate, few recaptures are obtained, but from about August 1st, when the juveniles begin to arrive, the numbers of recaptures usually increase because of a much slower turnover of birds on the shore. As is clear from Table 1, only very few adults are retaken after 2-3 days, whereas the recaptures of juveniles are much more evenly distributed. In 1963, no less than 18.3 per cent of all recaptured juveniles stayed more than 8 days. However, this phenomenon cannot simply be explained by an inherent difference in migratory urge between adults and juveniles. During the first half of August 1962, appreciable numbers of adults were still resting on the shore yielding as high proportions of recaptures as did the juveniles. Thus it still seems unclear why the migrating swarms pass much more hurriedly in the beginning of the season than later. Facts to be presented later indicate a somewhat increasing readiness to depart towards the end

Fig. 3. The relation between wing length and total weight in juvenile Dunlins trapped in 1963. The regression equation yielding expected weight at given wing length is $X = 0.59y + 3.63$.

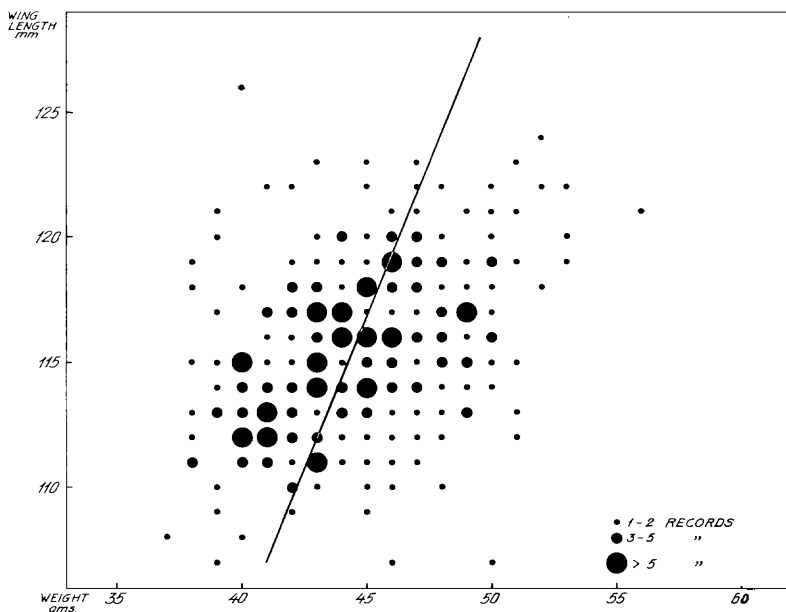


of the season, but this is hardly an unexpected trend in light of the stronger stimulation by weather factors, etc.

CALCULATION OF FAT STORES FROM TOTAL WEIGHTS

It has already been pointed out that the amount of accumulated fat in captured resting birds can be accurately calculated if the fat-free weight is subtracted from the total live weight. Unfortunately, there was no possibility in this case of performing the necessary extractions of samples of collected specimens to compute fat-free weights. No relevant data on waders are available in the literature as yet. Odum (in litt.) has kindly provided data on fat-free weights of some North American waders. Of five extracted Dunlins (*N. B.* of the larger subspecies *sakhalina*) collected at Sapelo Island, Georgia, during November-December, four specimens weighed between 39.66 and 43.64 gm, and one weighed 49.43 (uncorrected). These data, with the exception of the last, somewhat aberrant record, average about 4-6 gm more than the lowest total weights obtained from birds of similar wing lengths in the present material of *C. a. alpina*. This is probably explained by the larger body-size of the North American race, which apparently is not reflected in correspondingly larger wing measures. Thus for want of laboratory fat-free data on *C. a. alpina*, no exact computations of the magnitude

Fig. 4. The relation between wing length and total weight in adult Dunlins trapped in 1962-1963. The regression equation yielding expected weight at given wing length is $X = 0.41y + 7.52$.



of fat stores in the birds weighed at Ledsjär can be performed.

However, as the fat-free weight is relatively constant for birds of the same population and size, the gross variations in total live weight can be used as a measure of the varying amount of fat accumulated, if due correction is made for constitutional differences in over-all body size as indicated e.g. by the wing length. As is clear from investigations on passerine species, the mean fat-free weight increases with increasing wing length (Connell, Odum & Kale 1960). Thus, if small and large birds are supposed to accumulate about the same amount of fat (see below, p. 9-10), a corresponding increase in mean total weights will be found, which primarily reflects the relationship between fat-free weight and wing length to be corrected for. If this correction is not undertaken, the fat content of individuals larger than average will be overestimated, since the fat-free weight will be larger than average, whereas the fat content of small individuals is underestimated because of their lower fat-free weight.

Accordingly, total Dunlin weights as a function of wing lengths have been plotted in Figures 3 (adults trapped in 1962-1963) and 4 (juveniles trapped in 1963). Coefficients of correlation ($r \pm$ standard error of mean) and regression (b) as well as regression equations of expected total weight (w) at given wing length (l) were computed as follows:

adults	juveniles
$r = 0.33 \pm 0.05$	$r = 0.41 \pm 0.03$
$b = 0.41$	$b = 0.59$
$w = 0.41 l + 7.52$	$w = 0.59 l + 3.63$

The correlation and regression coefficients are statistically highly significant ($p < 0.001$) in both groups. There is an average rise in weight of 0.41 gm for each mm of increasing wing length in the adults as compared to 0.59 gm/mm in the juveniles. Between the extremes in wing length of about 110 and 125 mm there is a difference in mean weight of 6 gm in the adults and 9 gm in the juveniles. Generally speaking, the fact that the total weight rises with increasing wing length is due to a corresponding increase in fat-free body size. On the other hand, the considerable range of weights within each wing length category primarily depends on variations in fat storage. Blumenthal & Dolnik (1962) stressed that field weights of living birds are also influenced by the degree of fullness of the alimentary canal, but in comparison with the gross variations in fat supply, this variable is practically negligible. It can be estimated at roughly some 2 gm (1 gm in smaller passerines, cf. Helms & Drury 1960, Stolt & Mascher 1962) and will not cause a serious bias in the results, especially as the feeding-activity was quite evenly distributed throughout the 24-hour period (see p. 15).

The divergence in the weight - wing length relation between adults and juveniles is barely significant ($p = 0.02$). It should be noted that the contingents of adults and juveniles respectively may not wholly represent the same populations.

The calculations above are based on the assumption stated earlier that on an average birds of different size accumulate the same amount of fat. However, larger birds might perhaps be expected to have larger absolute fat deposits than smaller ones, the amount of fat accumulated being proportional to the size of the individual bird. This would give a flatter slope of the total weight regression line as compared to the fat-free curve (which here is assumed to be approximately represented in the distribution of the lowest weight records, cf. discussion on p. 10). In this case the regression lines computed would not adequately reflect the fat-free weight - wing length relation. However, the regression line in Figure 3 at least seems roughly parallel to the distribution of the lowest weights, indicating that the absolute amount of fat can be considered practically the same in all size groups. Nisbet, Drury & Baird (1963) analysed large samples of Blackpoll Warblers (*Dendroica striata*) and likewise stated that all size groups of that species had, on an average, the same amount of fat.

The calculated increase in mean weight of 0.59 gm per mm wing length in juvenile Dunlins is considerably larger than values given for passerine species by Connell, Odum & Kale (1960). Concerning "small and medium-sized" birds these authors found an increase of 0.30 gm per mm. This result is mainly based on measurements of fat-free weights in the Savannah Sparrow (*Passerculus sandwichensis*). For "large" birds an increase of about 0.40 gm is claimed, but

no measurements are given for species comparable in size to the Dunlin. Certainly, wide variations in the weight—wing length relation between different groups of species are to be expected. This is suggested also in the investigations by Nisbet, Drury & Baird on Blackpoll Warblers, referred to above. For this small-sized species (weighing on average 12-13 gm) an increase of only 0.10 gm. per mm wing length was calculated.

In the following all weight data have been corrected according to the corresponding wing length, unless otherwise stated. The mean wing lengths of 115.5 mm in the adults and 118.5 mm in the juveniles have been used as categories of reference, to which all data in each group have been levelled by subtracting (for larger birds) or adding (for smaller birds) an amount corresponding to the slope of the curves plotted in Figures 3 and 4.

Though no exact measures of the lipid reserves of the resting Dunlins could be achieved, some rough calculations can be based on the observed range of total weights as compared to available information on fat accumulation in migratory passerines. It should be noted that certain differences may exist between the patterns of premigratory fat accumulation in passerine and limicoline species. For want of further research no definite statement on this question can be made as yet. However, no large principal incongruencies are to be expected, as the internal and the external factors regulating the migrations of both groups of species will be basically the same.

As shown in Figure 3, the range of weight variation within each wing length group often amounts to 20-25 gm, which corresponds to about 40 per cent of the maximum total weight. (A group of birds ranging to 66 gm and with aberrant measures in October 1962 are not considered here, cf. p. 12). Thus the heaviest individuals, weighing about 60 gm, presumably had a fat supply of about 40 per cent, if the lowest corrected total weights of about 34-35 gm are roughly equal to the average fat-free weight of the population.

As a matter of fact, there are strong reasons for the assumption that the figures at the lower extreme of the range are very close to the real fat-free weight: 1. Investigations on passerines have shown that some records very close to—and even slightly lower than—the known fat-free weights are not uncommonly obtained among resting newly landed migrants (Voous 1957, Drury & Keith 1963, Nisbet, Drury & Baird 1963). 2. The lowest total weights obtained from the present material of *C. a. alpina* are somewhat lower than Odum's fat-free weights for the larger subspecies *sakhalina* (cf. p. 7), just as was to be expected if the former were close to the lean weight. 3. Further, a maximum proportion of 40 per cent accumulated fat conforms strikingly well to data given by other authors concerning several different genera in the Old and New World. Thus, Odum (1960 a, b) gives maximum fat values of 50 per cent of total weight in the Scarlet Tanager (*Piranga olivacea*) and the Bobolink (*Dolichonyx oryzivorus*) as well as 40 per cent in the Red-eyed Vireo (*Vireo olivaceus*), three species wintering south of the Gulf of Mexico and adapted to long non-stop over-water flights. For the Tennessee Warbler (*Vermivora peregrina*) and two *Dendroica* species Odum

(1958) has calculated maximum values of about 42 per cent. Williamson & Davis (1956) and Williamson (1958) reported over 50 per cent fat in Lapland Buntings (*Calcarius lapponicus*) and Wheat-ears (*Oenanthe oenanthe*). The comprehensive data on Blackpoll Warblers collected by Nisbet, Drury & Baird (1963) likewise indicate maximum fat reserves of 50 per cent. Drury & Keith (1963) give values of about 38-50 per cent fat for, among others, the Cat-bird (*Dumetella carolinensis*), two thrushes (*Catharus* sp.), a water-thrush (*Seiurus* sp.) and the American Redstart (*Setophaga ruticilla*), and Ward (1964) found maximum fat loads of 30-40 per cent in Yellow Wagtails (*Motacilla flava*) immediately before they started their spring migration from Nigeria. Finally, Wallgren (1954) found weight increments of 40 per cent in captive Ortolans (*Emberiza hortulana*), and Merkel (1958) has presented data on captive Red-backed Shrikes (*Lanius collurio*) corresponding to 50 per cent fat and on Robins (*Erithacus rubecula*) as well as two *Sylvia* species amounting to about 38-45 per cent of total body weight.

These very similar maximum fat values, recorded in many different migratory species in different parts of the world, seem to indicate that a fat content of 40-50 per cent forms an upper limit: still larger loads are likely to be energetically too uneconomical during longer flights.

In conclusion the lowest Dunlin weights of 34-35 gm can be assumed to correspond reasonably well to the average fat-free value for the populations concerned (of *Calidris a. alpina*). The mean fat deposition was 8-10 gm, or about 20 per cent of total body weight. As for the highest records of about 60 gm, the maximum fat deposition observed amounted to 25 gm or about 40 per cent of total body weight. These calculations conform very well with available information concerning several different passerine genera.

WEIGHTS OF ADULTS AND JUVENILES

In 1962, the adults at first capture weighed 44.5 gm on an average, as compared to 42.2 gm (uncorrected values) for the juveniles trapped before October. The wing lengths of the juveniles averaged larger (116.8 mm) than those of the adults (115.4 mm), but there was hardly any real difference in body size—the divergence was probably due to the more worn adult primaries. Although the sample of juveniles was fairly small (61 specimens) the difference in mean weights proved to be statistically significant ($p < 0.001$). Thus the larger adult weights probably reflected somewhat larger average fat stores. The larger weights of some aberrant juveniles trapped in October 1962 will be discussed in the next section. In 1963 there was no significant divergence of the initial weights between the two age groups, the juveniles averaging 44.0 gm and the adults 44.5 gm (uncorrected).

It has already been pointed out that the early contingents arriving in July, which consist mainly of adults, rest for only a comparatively short time on the shore before they depart (see Table 1). Though the initial weights of these contingents may be larger than in later occurring groups, these early birds in fact depart with much smaller

TABLE 2. MEANS AND RANGES OF TOTAL LENGTHS OF JUVENILE DUNLINS OBTAINED IN 1961-1963. SEE TEXT FOR DISCUSSION

		1961	1962	1963
July-Sept.	mean	178.2	179.1	178.4
	range	164 - 193(198)	167 - 192(199)	163 - 194
October	mean	184.5	185.3	—
	range	172 - 202	176 - 196	

average fat stores. During such short periods of rest no appreciable weight gain can be achieved.

No attempts to sex the trapped birds were made. There is no reason to suppose that the pattern of fat accumulation as displayed in the total weights will be different in the two sexes (cf. Connell, Odum & Kale 1960). Females probably weigh somewhat more, on average, than males on account of their larger body size. This is reflected in a slight tendency to a bimodal distribution especially of bill lengths and total lengths.

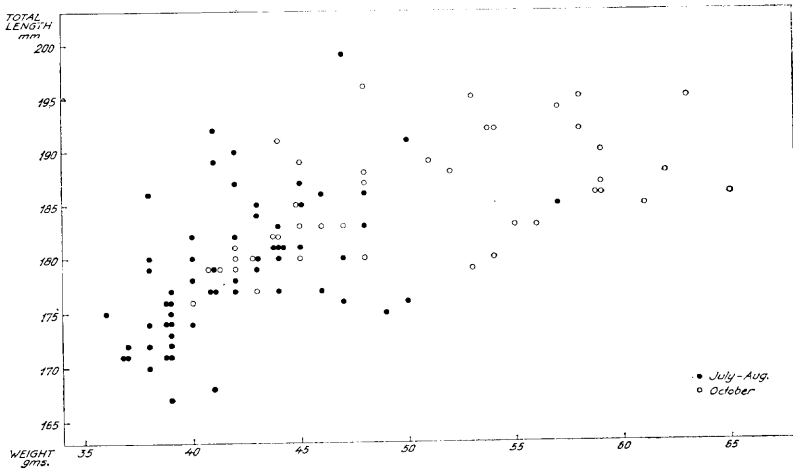
WEIGHTS AND MEASURES OF DIFFERENT DUNLIN CONTINGENTS

An analysis of measures taken in 1961 (when no weighings were performed), as well as of measures and weights in 1962-1963, revealed some conforming trends indicating the passage of a population of somewhat larger size and weight at the end of the season. The measurements will be more exhaustively accounted for in a later publication and are therefore only superficially referred to here.

The measure characteristics of the adults were in close conformity all the three years, showing negligible differences in mean wing length between 115.4 and 116.2 mm. Similarly, the somewhat greater wing lengths of the juveniles agreed fairly well throughout the three years. (The mean values varied between 117.0 (small sample), 117.4 and 118.5 mm). The difference between adults and juveniles is probably due to the more worn autumnal adult plumage. Concerning juvenile total lengths there was likewise good agreement with means between 178.2 and 179.1 mm during July-September. There were no marked changes in the measures during the course of this period. No counterpart was found to the birds of larger total lengths and shorter wings found at Ottenby Bird Station in late September 1957 (Martin-Löf 1958).

As is shown in Table 2, however, the mean of all total lengths in October 1961 (317 specimens) and in October 1962 (41 specimens) amounted to 184.5 and 185.3 mm, respectively. Compared to the means earlier in the same seasons, the differences are statistically highly significant ($p < 0.001$). But the real mean values of the larger birds are in fact likely to have been even higher. As will be shown, the October samples probably contained some individuals representing the population dominating earlier in the season.

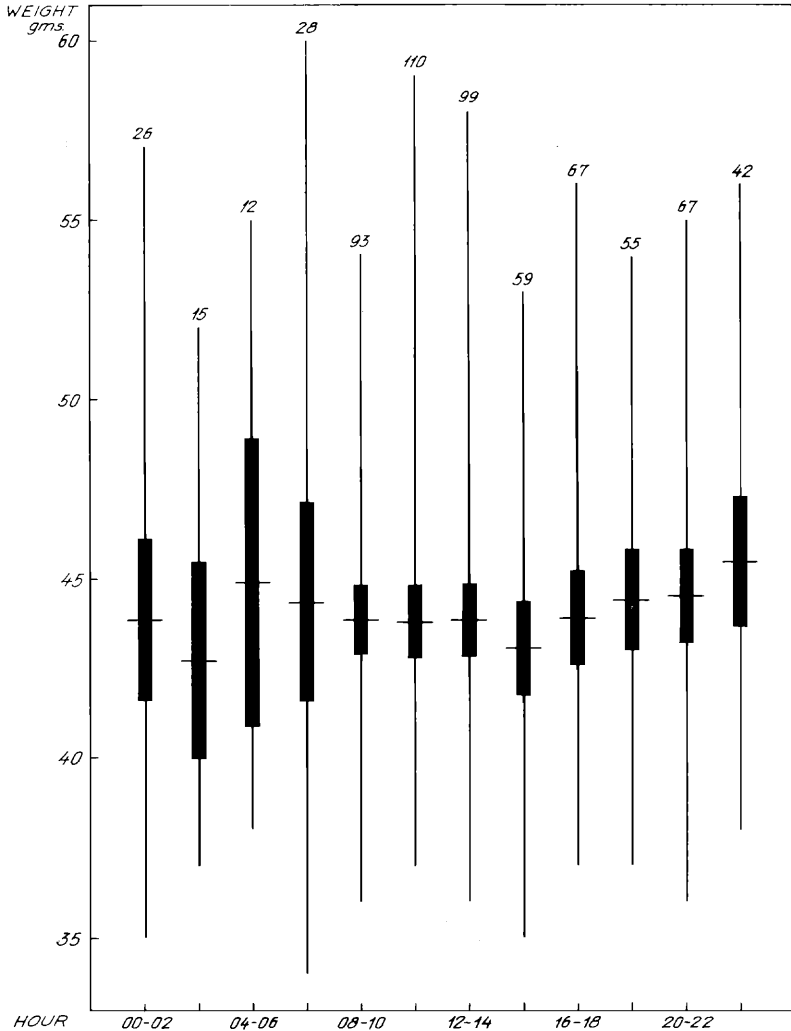
Fig. 5. The relation between total length and total weight in juvenile Dunlins obtained in July-August 1962 and in October 1962. Cf. Table 2 and see text for discussion.



The distribution of the weights obtained in October 1962 (Figure 5) show an apparent division of the values in two groups separated by a gap between 48-53 gm, where there are only two records. One group comprises 21 data well assembled below the level of 48 gm with a mean of 44.3 gm (uncorrected). The weights obtained during July-September averaged 42.2 gm, which conforms reasonably well with this group, but the remaining 20 October data ranging over 51 gm do not fit in with this picture. There was only one record ranging over 50 gm earlier in the season of 1962, whereas some of the October birds even exceeded 60 gm with one extreme at 65. It should be noted that these weights were disproportionately large, even when the larger size of the birds (as indicated by total length) was taken into account. In August-September 1963 some weights ranging up to 60-61 gm were recorded, but there was no aberration of total lengths in the birds concerned. Total weights obtained in England between August-April often range over 60-65 gm (cf. Figure 8), but most of these data are obtained from populations on their winter grounds. Moreover, they may partly represent different populations.

The October wing lengths showed no significant differences compared to measures obtained earlier in the season. Likewise, an analysis of bill lengths showed no significant variations in the means. Thus the greater total lengths of October were not due to longer bills in these birds, but seemed primarily to depend on a constitutional difference in body size, not reflected in other measures taken. (There was in fact a slight tendency to somewhat larger wing and bill measures, which might have proved significant with larger samples). This stresses the fact that wing length does not always

Fig. 6. Diurnal weight variations in resting juvenile Dunlins. Weight data (corrected to the mean wing length) are shown for each two-hour period. Vertical line: Range of weights. Horizontal line: Mean weight. Solid rectangle: Standard error of mean. Figure at top of each graph: Number of weighings.



adequately reflect differences in body size between different populations. The correlation may even turn out negative, in accordance with the rules of Allen and Bergman (in Lister 1962, cf. Martin-Löf 1958). Thus it may be important to take other measures as well.

In conclusion, concerning the distribution of weights and total

lengths of the Dunlin contingents in October 1962, there was apparently a combination of one group largely corresponding in weights and measures to the populations occurring earlier in the season and one aberrant group of larger weight and total length, other measures being mainly equal. However, the material is scanty, and since it is impossible to classify all individuals with certainty, no reliable characteristics of weight and measures can be given for the last-mentioned group. These larger birds possibly represent a different population appearing at the end of the season. Whether their larger weights depend on higher average fat-free weights or on larger average fat stores remains to be investigated.

Unfortunately, no trapping was possible in October 1963, but just as in earlier years no birds with a similar combination of large measures and large weights occurred before the end of September. The large total lengths in October 1961 (equal to those of October 1962) indicate that similar birds took part in the passage this year too. Further studies on these late aberrant Dunlin contingents are being carried on.

DIURNAL WEIGHT VARIATIONS

To calculate the diurnal variations in body weight, two-hour means were plotted as shown in Figure 6. There are no striking fluctuations. The smaller deviations in the early hours as well as between 1400-1600 and 2200-2400 are not significant.

Investigations on passerines have often shown a consistent diurnal variation with a marked loss during the night and a rapid gain in the early morning hours, followed by a flattened out curve slightly rising until the afternoon (Linsdale & Sumner 1934 a, Baldwin & Kendeigh 1938, Helms & Drury 1960, Stolt & Mascher 1962 and others). The flattened out 24-hour curve of the Dunlin weights might well depend on a more evenly distributed diurnal activity. Periods of rest and activity may alternate at any time of the day and night. In contrast to this, passerine species usually have a distinct nightly period of rest when they lose weight uninterruptedly until feeding activity starts again in the morning. This is true even for resting migrants (see e.g. Stolt & Mascher 1962).

Concerning the individual diurnal changes, as judged from weighings of the same birds twice or more times within 24 hours, there are widely diverging patterns. No general trend can be ascertained except perhaps a somewhat more restricted range of variation during the middle of the day. In order to analyse the individual over-night fluctuations in weight, 33 birds, weighed between 1800 and 2200 and reweighed next morning between 0200 and 0600, were picked out. Of these 9 showed on an average an increase of about 1.7 gm, 16 a decrease of 1.5 gm. The remaining 8 specimens did not change their weights at all. This clearly stresses the individually very different activity rhythms, which may of course also vary from day to day in the same bird.

It is interesting to compare these results with the recent comprehensive investigations by Ehlert (1964) on the diurnal feeding-

activity of Dunlins resting at the Isle of Mellum off the German North Sea coast. As was evident from his field observations as well as his analyses of ventricle-contents, there was a slight tendency to longer periods of rest during the afternoon, though the influence of the tide was much more important. Ehlert did not perform weighings of his birds, but as has been stated earlier e.g. by Witherby *et al.* (1949), there was also feeding activity during the night. This is consistent with the weight data presented here.

The observed individual range of variation within a 24-hour period amounted to 5 gm at the most, which was recorded in three birds. This is equal to 10-11 per cent of the total body weight in these three cases. Quite similar proportional weight fluctuations have been found in different passerine species, studied e.g. by Baldwin & Kendeigh (1938), Schildmacher (1952), Helms & Drury (1960), Blumenthal & Dolnik (1962) and Stolt & Mascher (1962).

DAILY WEIGHT FLUCTUATIONS

In 1962 the daily trapping figures were generally too low to justify a statistical treatment.

Mean weights were computed for all days in 1963 with 15 records or more. If there were two or more records of the same bird on one day, the average weight was taken. Only on three days were there enough adults to justify computation of mean values, namely on July 10th, 16th and 26th. The differences were quite negligible, varying between 44.8 and 45.3 gm. As these figures are corrected to the adult mean wing length of 116 mm, they are not directly comparable to the juvenile weights.

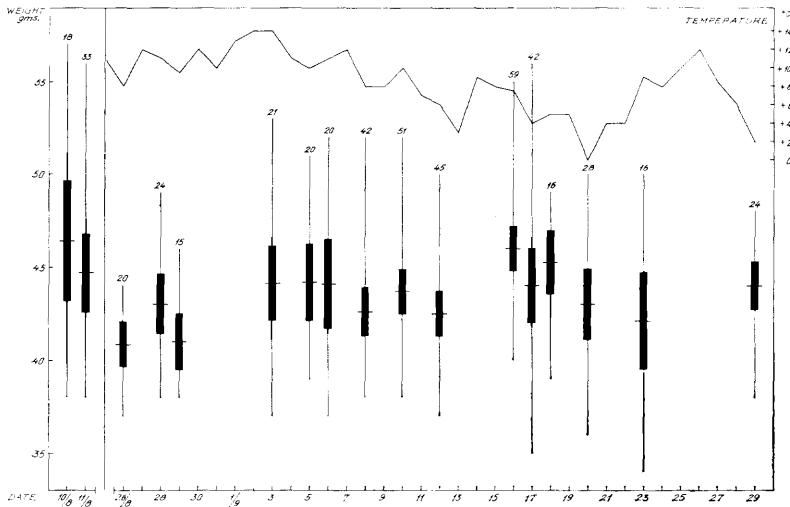
Mean weights of juveniles were computed for 15 days as shown in Figure 7. There are no very striking differences, though the weights of August 26th, 28th, and 29th seem to form a group of somewhat lower mean values, and those of September 16th, 17th, and 18th another group of somewhat higher means. Concerning the lower August weights, averaging between 40.8 and 42.7 gm, it should be stressed that a large proportion of the birds trapped on these days had just arrived (cf. Figure 2)—there had been no Dunlins on the shore for about a week. The larger September weights averaging between 44.1 and 45.8 gm are more difficult to account for.

INFLUENCE OF WEATHER ON DAILY WEIGHTS

There was no correlation between general weather conditions (cloudiness, fog and precipitation) and weights as found in resting Starlings (*Sturnus vulgaris*) by Svensson (1964). According to this author, Starlings decrease in weight during days with "bad" weather perhaps because their feeding activity is suppressed, or because of scarcity of food under such conditions. However, this does not seem to be a general phenomenon: Nisbet, Drury & Baird (1963) found appreciable gains in weight in resting Blackpoll Warblers during rainstorms.

Unless extreme conditions prevail, there is hardly any tendency towards suppressed feeding activity in resting Dunlins during per-

Fig. 7. Daily weight figures of migrating juvenile Dunlins in 1963 compared with minimum temperatures. The weight data are corrected to the mean wing length. Vertical line: Range of weights. Horizontal line: Mean weight. Solid rectangle: Standard error of mean. Figure at top of each graph: Number of weighings. No computations have been performed for days with less than 15 weight records.



iods of "bad" weather (cf. Ehlert 1964). However, the migratory activity may increase under such conditions, and this, in turn, may interfere with the feeding activity. This question will be discussed later. Whether the availability of food on the shore is influenced to a marked degree by changes in general weather conditions is unknown. In any case no such fluctuations were reflected in Dunlin weights.

Concerning the day-to-day temperature fluctuations (cf. Figure 7) there seems to be a slight tendency to lower weights during cold spells. Between August 26th and September 23rd, when daily mean figures could be more continuously worked out, 8 temperature falls occurred. Of these, six were accompanied by slight decreases in mean weights amounting to 1-2 gm, whereas one seemed without effect and one could not be judged for want of weight data.

A positive correlation between weight and temperature was found also by Svensson (1964) for Starlings on autumn migration. Svensson stresses that several earlier investigations have revealed a negative correlation between weights and temperature in the winter season (Baldwin & Kendeigh 1938, Seibert 1949, Odum 1949, Owen 1954, Helms & Drury 1960) but, this may hold true only as long as food is available in unlimited amounts, otherwise the correlation may turn out positive (Haftorn 1951, Kluijver 1952). This would seem to indicate that there was perhaps less food available for the Dunlins at lower temperatures. But such an explanation is doubtful in this case. Firstly, the temperature falls occurred at very different

mean levels, whereas no correlation was found between mean weights and the general temperature level during different periods. Secondly, it should be noted that most of the studies cited were performed during winter conditions. Other factors may regulate, e.g. food intake and reactions to meteorological variables during migratory periods when different physiological controls become operative (Helms & Drury 1960, King 1961 a, b, 1963, King, Barker & Farner 1963). If resting migrants react on temperature falls with increased "migratory unrest"—as is commonly the case in autumn—this may interfere with their usual feeding activity, resulting in corresponding slight decreases in weight. Naturally, birds which are initially in a sufficiently strong "migratory mood" may even be stimulated by the weather change to leave the resting-grounds. There is in fact a tendency during both seasons for larger Dunlin departures to coincide with marked temperature drops (cf. Figures 1 and 2). As will be shown later, heavier birds with large fat stores most readily leave (cf. p. 27), and at the same time new contingents of birds in leaner condition arrive. This also tends to lower the average weight of the resting population during or immediately after cold spells.

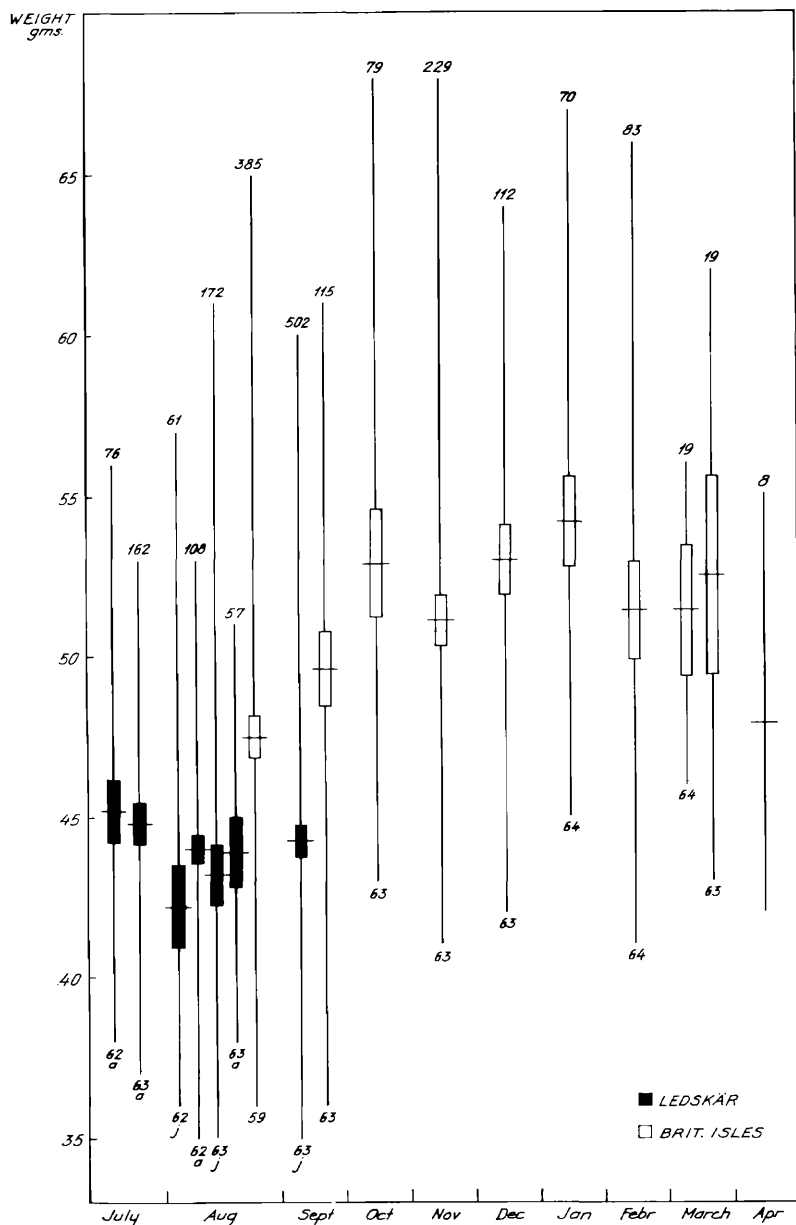
Thus weight variations recorded in a resting population in connection with weather changes may depend largely on variations in the rate of turnover of birds and their degree of migratory activation. Obviously, this does not rule out possible direct influences of various external factors on feeding activity, food availability, etc., which may manifest themselves in body weights.

No meteorological variables except temperature could be correlated to the weights. It should be noted that the simultaneous changes of several meteorological variables often makes an analysis of the possible influence of one separate factor very difficult.

SEASONAL VARIATIONS IN WEIGHT

Mean weights for each month during the course of the season at Ledsjär are shown in Figure 8. The difference between adults and juveniles has already been mentioned (p. 11). In addition, some British weight data—kindly provided by Mr. H. Boyd (in litt.) at the Wildfowl Trust—have been included, showing weight variations during the course of the autumn and winter seasons until the beginning of spring migration. These data have been collected partly by the Wash Wader Ringing Group (Aug.-Sept.) and partly by Mr. W. A. Cook for the Wildfowl Trust (Oct.-April). The values have not been corrected according to wing lengths, but the rough distribution of measures was unaltered throughout the whole period. Obviously, the weight records obtained at Ledsjär and in Britain should be compared very cautiously, as different populations of birds may be concerned to a large extent. It is noteworthy that only 18 per cent of all winter recoveries of Swedish-ringed Dunlins have been reported from the British Isles, as compared with 33 per cent of Norwegian-ringed recoveries (computed from Ogilvie 1963). As a consequence, the significant differences in mean weights between birds obtained at Ledsjär during July-September and in Britain

Fig. 8. Seasonal variations in weight at Ledskär (solid) and in the British Isles (open). British data provided by Mr. H. Boyd at the Wildfowl Trust. Weight data are shown for each month in different years. Vertical line: Range of weights. Horizontal line: Mean weight. Solid or open rectangle: Standard error of mean. Figures at top of each graph: Number of weighings. Figures at the bottom: Year. a = adults, j = juveniles. The British data were not analysed as to age.



during August-April cannot quite safely be interpreted as depending on an increase of weight in birds which have arrived at their winter-grounds, though the gradually increasing mean values during August-October in Britain might support such an explanation.

In any case there is no conspicuous loss of weight after the end of the fall migratory period. On the contrary, the Dunlins resting in the British Isles seem to maintain appreciable fat stores throughout the winter. This is probably in conformity with the winter fat storage occurring in passerine species (Linsdale & Sumner 1934 a, Baldwin & Kendeigh 1938, Nice 1938, 1946, Odum 1949, Weise 1956, 1963, Helms & Drury 1960, King & Wales 1964, and others).

Many passerine birds lose much of their fat after the autumn migratory period, which results in a pronounced loss of weight. However, especially such species or populations as migrate only comparatively short distances and winter in temperate areas may maintain appreciable fat stores as an adaptation to the harder climatic conditions prevailing farther north (cf. Odum & Perkinson 1951, Wagner 1963). Cold spells are accompanied by peaks in the fat deposition, provided, of course, that the supply of food is unlimited.

The winter fat is mainly deposited subcutaneously (Odum & Perkinson 1951). This fat is obviously of great importance for the survival of the birds, acting as an isolating "coat", forming an important energy reserve during periods of food scarcity, and meeting the larger requirements of energy necessary to maintain basic physiological functions. In addition, the maintenance of appreciable fat stores throughout the winter might be a prophylactic adaptation for the performance of "hard weather movements" which are initiated especially by cold spells with frost and snow during the course of the winter. Such movements between the regular fall and spring migratory periods (= German *Zwischenzug*) do not uncommonly occur in the British Isles, and waders often participate to a large extent, as stressed e.g. by Witherby et al. (1949), Lack & Eastwood (1962) and Lack (1963).

Lack (1960) stated that hard weather movements are not likely to be preceded by a deposition of peritoneal fat stores beforehand, and that this in such case constitutes a difference from true migration. However, if considerable fat stores are maintained throughout the winter, the birds will be prepared to move considerable distances at any time, if an adequate stimulus (e.g. weather change) occurs. Birds wintering in areas where they are subjected to climatic hazards may keep a sustained "migratory readiness" during the winter months (cf. Dorst 1962) enabling them to escape from inconvenient weather conditions. Thus a cold spell will principally exert the same effect on them—eliciting a southward movement—if it occurs during or between the autumn and spring migratory periods.

It remains to be investigated if such stores of winter fat occur also in other shore-birds wintering in similar climatic zones, and if this fat corresponds chemically and distributionally to the "winter fat" or the "migratory fat" occurring in passerines (cf. McGreal & Farner 1956, Odum 1960 b, Walker 1964).

Odum (in litt.) states that none of the shorebirds of different genera he has extracted so far have proved to be particularly fat. Of five specimens of *Calidris alpina sakhalina* collected in November-December, none had a fat content exceeding 13 per cent. They were taken at Sapelo Island, Georgia, about 31° 20' N latitude. It would be of interest to investigate winter weights of palaeartic Dunlin populations moving farther south to warmer areas. A smaller proportion of Swedish-ringed birds winter in Portugal and Spain, and there are even records from NW. Africa (Ogilvie 1963) at latitudes corresponding to Georgia. Such contingents, wintering in areas where climatic stresses are negligible, should not have the same need for keeping large fat stores between the autumn and spring migratory periods. It has been shown by Ward (1964) that Yellow Wagtails wintering in Nigeria have very low fat contents, about 5 per cent only. Immediately before their departure, however, a rapid fat deposition takes place, which may amount to 30-40 per cent. In the Congo, Curry-Lindahl (1961a) found a slower weight gain in Yellow Wagtails before departing.

RECAPTURE WEIGHTS

Adults.

In 1962, 172 adults were trapped. Of these 31, or 18.0 per cent, were recaptured later, yielding in all 43 recapture weights. The only bird retaken after more than 11 days was caught on the 21st day. Possibly, such comparatively extreme resting-times are to be considered abnormal, indicating injuries or sickness in the birds concerned.

In 1963, 220 adults were trapped. 32, or 14.5 per cent, were recaptured, yielding 42 recapture weights. Only two birds were retaken after the 3rd day, one on the 5th and one on the 7th day. The strikingly longer average resting times recorded in 1962 (cf. Table 1) probably depended on the duration of the adult passage that year. There were still many adult birds on the shore until the middle of August, when resting times generally seem to increase markedly as compared to July. In 1963, however, the passage of adults ended in the last week of July.

Both years the initial mean weights of the birds retaken later were slightly lower than those of the birds not retaken. In 1962, the mean weight of the birds not recaptured amounted to 44.7 gm (uncorrected) whereas the recaptured birds averaged 43.6 gm initially. The difference was somewhat more pronounced in 1963: 44.5 gm and 42.9 gm respectively.

Concerning the possible reason for the larger weights of birds not retaken, it should be stressed that a considerable number of them might already have been resting on the shore for some time without entering the traps. The recaptured group, on the other hand, might have contained a relatively larger proportion of newly arrived, lighter birds. Unfortunately it is impossible to make reliable estimates of these proportions in the present material. Thus, the related figures cannot be directly used as a support for the assumption

that birds arriving in leaner condition stay longer than initially fatter birds. Nevertheless, other data to be presented later indicate that this is in fact the case.

The adults generally stayed too short a time on the shore to achieve any larger weight gains (cf. Table 1). The recaptures of 1962 showed no significant gain in weight during the time of rest on the shore. Their average weight after 2 days (21 records) was 44.6 gm as compared to the initial figure of 44.0 gm. In 1963, only 11 birds were retaken after the 2nd day. Their mean value amounted to 44.9 gm as compared to the initial 42.9 gm. This difference is however also not significant.

The material on adult recaptures is too scanty to justify more elaborate statistical analyses.

Juveniles.

In 1962, 102 juveniles were trapped. If the aberrant October group is excluded, there are 61 left to be considered. 28, or 45.9 per cent, were recaptured later, yielding in all 48 recapture weighings. The recaptures were evenly distributed over the first five days after ringing, but only 3 birds were retrapped after the 5th day. The mean initial weight of the recaptured birds was 40.3 gm. as compared to 42.2 gm for the group not recaptured. There was a slight gain of weight during the time spent on the shore. The recaptures obtained after more than two days averaged 43.2 gm. It should be stressed that the samples of 1962 are small and the differences barely significant.

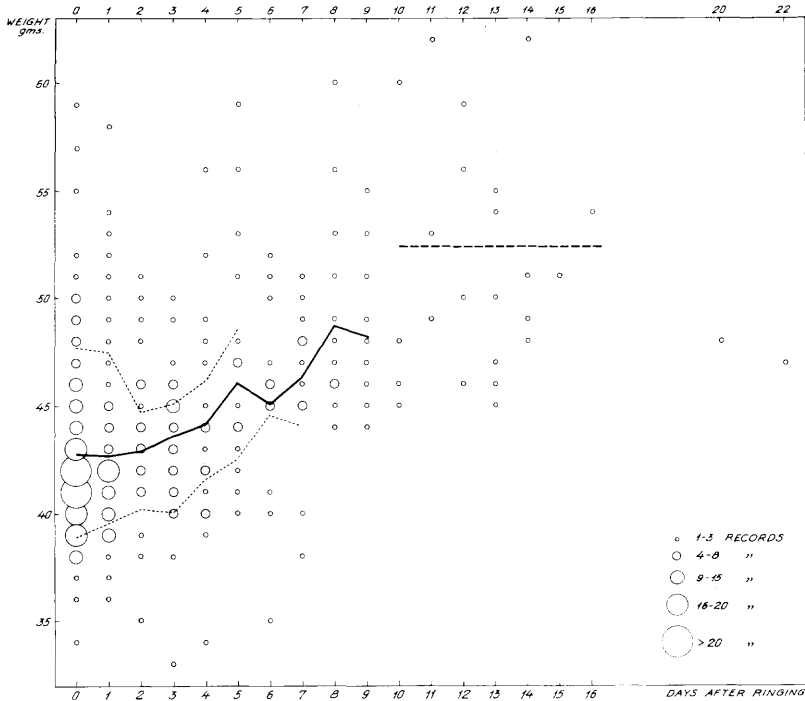
In 1963, 672 juveniles were ringed. 197, or 29.3 per cent, were recaptured later. In all, 333 recapture weighings were obtained. 36, or 18.3 per cent, of all recaptured birds stayed more than 8 days and 4 stayed more than 14 days. They were caught on the 15th, 16th, 20th and 22nd day respectively. There were no conspicuous fluctuations in the average time of rest during the course of the season. Relatively more retrappings were obtained of a contingent present on the shore during the last week of August, but this seems to be the result of a generally higher trapping efficiency at that time.

The mean weight obtained from the first weighing of the birds later recaptured was 42.6 gm, whereas the group not recaptured averaged 44.3. As has already been pointed out, this divergence might largely depend on different proportions of newly arrived birds in the two groups.

The change of weight during the time spent resting and feeding on the shore is shown in Figure 9. Means have been computed for each day from all weights obtained from Day 0 (the day of ringing) to Day 9. The 28 values after more than 9 days have been lumped together.

There is an obvious general rise in weight, but it should be noted that no trend is clear until the 3rd day. From then on the weight increases steadily at a rate of about 1 gm a day. From the initial mean weight of 42.6 gm an average of 52.4 gm is reached after Day 9.

Fig. 9. Weight variations in recaptured juvenile Dunlins. The weight data are corrected to the mean wing length. Solid line: Mean weights for each day of rest on the shore, including all recapture data. Barred line: Mean weight of all recaptures obtained after 9 days. Upper and lower dotted lines: Mean weights of the initially heaviest and lightest birds, respectively (see text for further explanation). Day 0 is the day of ringing.



As a comparison, daily weight gains in some resting passerines have been calculated from some data given in the literature. According to Bryson (1951) Chaffinches (*Fringilla coelebs*) arriving at the Isle of May gained on an average about 17 per cent in weight during the 3rd to the 8th day after the first capture. A computation, from all his recaptures, of the daily weight gain gives an average gain of 0.7 gm per day. An interpretation of the records by Williamson & Butterfield (1952) on Willow Warblers (*Phylloscopus trochilus*) yields a mean daily weight gain of about 0.35 gm. The data given by Williamson (1956) on the Greenland Redpoll (*Carduelis flammea rostrata*) likewise point to an average daily gain of 0.35 gm. Odum & Perkinson (1951) found a daily increase of about 0.47 gm in White-throated Sparrows on their winter-grounds immediately before departing. Finally, the most comprehensive material of recapture weights available, that of Nisbet, Drury & Baird (1963) on the Blackpoll Warbler, has been graphically analysed to compute the

daily weight gain from the second until the 7th day (on the first day there was generally a decrease). A rise of weight of approximately 0.4 gm is arrived at. If the phenomenon of initial weight loss found e.g. by these authors, by Davis (1962) and in the present investigation is generally occurring, the figures cited—except the two last-mentioned—are certainly somewhat too low, since the first one or two days of rest of newly landed migrants should not be taken into account. An average weight gain of about 0.4-0.8 gm per day thus seems to be common among resting passerine migrants of smaller size. But, obviously, there will be a more rapid gain in highly starved out birds and a slower gain—if any—in birds arriving in better condition after shorter flights. In one of Bryson's (1951) Chaffinches a daily gain of 1.2 gm was recorded, Blumenthal & Dolnik (1962) stated that finches can store up 1-1.5 gm of surplus fat in 24 hours, and Davis' (1962) maximum figures of weight increase in Robins (*Erithacus rubecula*) amount to no less than 3.7 gm per day.

However, it is important to evaluate individual day-to-day weight changes in connection with the passerine diurnal weight rhythm (cf. p. 15) so that the effect of the time of day is ruled out. Observed maximum daily weight gains in the Dunlins studied amounted to 3 gm. Because of the individually widely diverging diurnal weight variations, this figure is still more difficult to evaluate.

In order to analyse if there were any differences in the pattern of fat accumulation between initially leaner and initially fatter Dunlins, the 50 lightest as well as the 50 heaviest birds were picked out. For each group separately, mean weights were computed in the same way as earlier described for the whole material (cf. Figure 9, dotted curves). This reveals an interesting divergence in the trend of the two mean curves, which is obscured when the entire material is lumped together. The lightest group gains weight steadily from the first day (with 6 individual exceptions showing slight decreases) until the mean level for the whole material is approximated after the 9th day. The heavy birds, on the other hand, show a remarkable decline during the first two days. The average decrease is about 3 gm with individual extremes at 6 gm (3 records). The difference is statistically significant ($p < 0.001$) when Day 2 and Day 3 are added together. From Day 3 the weight rises again, almost as rapidly as in the lighter group. Apparently, there is no very marked difference in the rate of weight gain between leaner birds and fatter ones. By Day 4-5 the initial weight at the first capture is regained.

In fact, the initial weight loss is certainly even greater in the fattest birds than indicated by these computations. Among birds which have much fat at the first capture, there will always be a number of individuals which have been resting for more than 1-2 days on the shore before being trapped. If they are caught on the third day after arrival or later, their period of weight loss is already passed, and they will show a rise in weight from Day 0. As for the observed individual weight losses during the first two days after the initial capture, it will be realistic to assume an average weight loss of 4 gm as far as the heaviest birds are concerned. Some individual weight variations in birds which were trapped several

TABLE 3. INDIVIDUAL WEIGHT VARIATIONS IN SOME CASES, WHICH CLEARLY DISPLAY THE PHENOMENON OF INITIAL WEIGHT LOSS. ALL WEIGHTS ARE UNCORRECTED. DAY 0 IS THE DAY OF RINGING

Day	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Case 1	48.0	42.0	41.5	41.5	42.0	45.0							46.0	
Case 2	45.0	41.5		41.0			43.0							
No. 3	45.0	40.5			40.0		40.0				44.0			49.0
4	42.5	42.0	40.0			44.0								
5	42.5	40.0		40.0		44.0								

times during the first week are exemplified in Table 3. The phenomenon of initial weight loss is clearly displayed. It is evident that when there is a considerable loss of weight during the first few days, the initial weight level is not always regained even within a week.

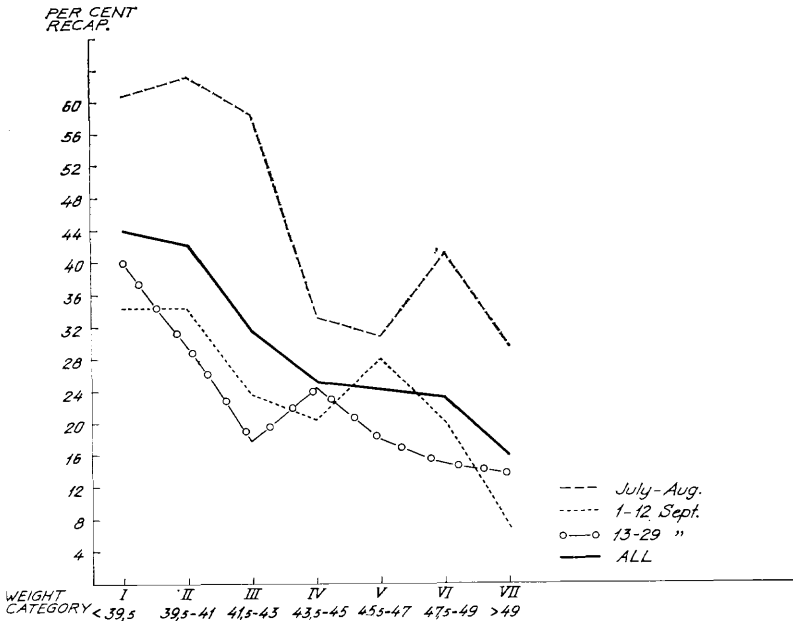
It is of interest to compare these variations in recapture weights with some results of earlier investigations on passerines. Davis (1962) recorded loss of weight in migrating Robins immediately after landing, both in spring and autumn. The comprehensive investigations on migrating Blackpool Warblers by Nisbet, Drury & Baird (1963) on the whole yielded the same results. They found a loss of weight on the first day after banding, followed by a continuous increase during the subsequent days. By the third day the initial weight level was reached. In addition, reference should be made to the studies on White-throated Sparrows by Wolfson (1954 a), cf. Wolfson & Winchester (1960). When birds were brought into captivity and held under natural day lengths, those with heavy fat deposits initially lost weight while those without much fat gained weight (which, among other facts, rules out a possible effect of capture and handling).

These quite similar observations on three different passerines as well as on a limicoline species suggest that the phenomenon of initial weight loss occurs quite generally, at least in migrants which arrive with relatively well preserved fat stores.

In conclusion, Dunlins arriving with appreciable fat stores decrease in weight during the first two days after the initial capture, in contrast to light individuals which gain weight steadily from their arrival on the shore.

A feasible explanation of this divergence between the two groups is that birds which arrive with well preserved fat stores are still in a "migratory mood" (*Zugstimmung*) which causes them to waste much time and energy on "migratory unrest" activities, as is often observed on resting-places for waders. After a couple of days they calm down to concentrate more on feeding activities. The mean total weight of the heavy group investigated in this case amounted to 47.7 gm, which corresponds to about 13 gm fat or 28 per cent of total body weight, assuming (as above, p. 11) an average fat-free

Fig. 10. Percentage of recaptures obtained of birds of different initial weights, i.e. fat stores. The weight data have been arbitrarily divided into VII categories (cf. the text).



weight of about 34-35 gm. In contrast to this, the lighter group averaged 38.8 gm, corresponding to about 4 gm or 10 per cent fat only. The average fat content in non-migrating passerine species is of the order of about 4-6 per cent (Odum 1960 a, Ward 1964). As these birds had thus used up a considerable part of their fat reserves before their arrival, they were presumably in a condition of weaker "migratory mood", which was overshadowed by a stronger impulse to feed as soon as they had landed.

The theory just presented presupposes a positive correlation between the amount of fat accumulated and the strength of the migratory urge. It has been claimed earlier by some authors (e.g. Odum & Perkinson 1951, Merkel 1958) that a certain level of fat deposition has to be achieved before migration starts. This may be true in some cases, but as pointed out by Putzig (1939), Wallgren (1954) and Millar (1960), and as shown by Kendeigh, West & Cox (1960), Blumenthal (1961), Johnston (1962), Wagner (1963), King & Farner (1963), Weise (1963) and Lofts, Marshall & Wolfson (1963) it is not always so (cf. also Mewaldt, Morton & Brown 1964).

To ascertain possible influences of the magnitude of fat stores on the migratory readiness of Dunlins, all birds were grouped into 7 different weight categories according to their corrected initial weight (see Figure 10). The lightest category of weight was below

39 gm, corresponding to 5 gm fat or less, and the heaviest group exceeded 49.5 gm. The proportion of recaptures obtained of each category was plotted as shown in Figure 10.

The mean curve computed for the whole season declines steadily with increasing weights from weight category II. Starting with an initial percentage of recaptures as high as 42-44, the proportion drops to 15-16 per cent in category VII. Thus there is obviously a positive correlation between the amount of accumulated fat and the readiness to migrate. However, it cannot be stated that a certain amount of fat is a necessary prerequisite for departing. Though the mean curve for the whole season seems to indicate that a marked decrease in the number of resting birds does not occur until they reach the third weight category, this is not generally the case. If the season is divided into three periods according to an arbitrary division of the Dunlin passage into three main contingents (of which only the first one—in early August—is really quite distinct from the others), it becomes clear that considerable variations occur.

The July-August contingents seem to have been lingering on the shore until weight category IV (equal to 9-10 gm fat) was reached. Then a rapid decline in the percentage of recaptures obtained, from about 60 to 32 per cent, indicated a markedly increased readiness to depart. The curve computed for early September shows a decrease in the percentage of recaptures in weight category III, and in late September the decline already occurs in weight category II (equal to 5-6 gm fat). This also indicates an increased readiness to depart with smaller fat deposits towards the end of the season. This might depend either on an increasing strength of the migratory urge in the juveniles during the course of the season, or on increasing external stimulation, e.g. from lower temperatures and other meteorological factors, or both.

As no reasonably accurate figures for the trapping efficiency (which varies widely, e.g. with fluctuations in water level and weather conditions) can be calculated, it is unknown to what extent even birds of weight category I may possibly continue their migration. The generally larger proportion of recaptures in July-August (cf. Figure 10), as compared to September, might have depended on a higher trapping efficiency and on somewhat longer periods of rest. However, considering the generally rapid passage and short resting periods of the adults in July (discussed above, cf. Table 1), it is evident that Dunlins may readily depart with comparatively small fat reserves of only a few gm.

POTENTIAL FLIGHT RANGES

As no data are as yet available on the energy expenditure of limicoline birds during flight, nothing can be definitely stated concerning the possible non-stop flight ranges of the Dunlins studied. In some larger passerines (*Hylocichla* spp.) fat losses of roughly 1.8 per cent of total weight/hour during migratory flight have been calculated (Graber & Graber 1962). Assuming a similar magnitude of fat loss in Dunlins with maximally 25 gm fat, i.e. 40 per cent of

total weight, they would be able to fly non-stop for some 25-30 hours, which is certainly no overestimate. Thus, a Turnstone (*Arenaria interpres*) ringed at Heligoland was recovered in France 25 hours later after travelling at least 820 km (Dorst 1962). Assuming further a still-air speed in smaller wader species of about 50 km/hour (cf. Meinertzhagen 1955), maximum flight distances would amount to some 1250-1500 km, e.g. from south Sweden to the Atlantic coasts of Britain and N. France. It is possible, however, that waders do not deplete their energy reserves as rapidly as passerines, since they are probably stronger flyers with more efficient aerodynamic capacities. Thus the potential flight ranges—which are probably seldom made full use of—may be still larger in the Dunlins studied, but this point needs special investigation.

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SUMMARY

During two consecutive seasons Dunlins (*Calidris a. alpina*) on autumn migration in south Sweden were weighed and measured at the Ledsjär Bird Station in the province of Uppland. In this paper primarily the weight data are analysed. All weights were corrected according to the size (wing length) of the birds. A comparison of the results with available information on passerine species is made.

1. The Dunlin occurs regularly on autumn migration at Ledsjär from early July until early (or in some years the middle of) October. The adult population dominates in number until early August. Almost exclusively juveniles occur during September-October. In certain years there is a distinct gap which may amount to one week or more between the occurrences of the two age groups.
2. As is clear from the recapture figures, the passage proceeds much faster early in the season than later. In 1963, only 14.5 per cent of the adults—which form the bulk of the earliest contingents—were retrapped as compared to nearly 30 per cent of the later-arriving juveniles. Very few adults stayed more than 2-3 days, whereas 18.3 per cent of all recaptured juveniles lingered more than 8 days. However, this discrepancy does not

seem to depend on a stronger migratory urge in the adults. In 1962, many adults still rested on the shore in early August, yielding as large a proportion of recaptures as the juveniles. Towards the end of the season the juveniles showed a somewhat increasing readiness to depart.

3. During both years, the initial weights of the adults averaged slightly more than those of the juveniles. However, as the resting-periods of the adults passing early in the season were much shorter, they departed in a much leaner condition, on an average, than did the juveniles.
4. An increase in total weight of 0.59 gm per mm wing length was found in the juveniles. This is appreciably more than the figures applying to medium-sized and larger passerines. In adult Dunlins, a somewhat smaller increase amounting to 0.41 gm per mm wing length was found, but the difference is barely significant.
5. The highest weight records obtained were probably near the fat-free weight of the subspecies *C. a. alpina*, which is likely to average about 34-35 gm. Some fat-free data on the larger *sakhalina* subspecies averaged about 5 gm more than the fat-free weight calculated for the corresponding wing length in *C. a. alpina*. The maximum fat deposition in Dunlins resting at Ledsjär amounted to 20-25 gm fat or 40 per cent of total body weight, which is in accordance with data published on passerine migrants.
6. In October 1962, a Dunlin contingent of larger weights and total lengths occurred, mixed with representatives of the population dominating earlier in the season. Total lengths taken in October 1961 indicate the presence of similar birds also that year. There were no significant differences in other measures.
7. No significant diurnal variations in weights were noted. This is consistent with findings in the field, which indicate that the activity of Dunlins and related waders continues to a considerable extent throughout the night hours. Investigations on ventricle-contents support this view. An analysis of individual over-night changes showed widely varying patterns. The individual range of weight variation within 24 hours amounted to at most 5 gm, or 10-11 per cent of total body weight. Proportionally, this corresponds well to the diurnal fluctuations occurring in passerines.
8. Day-to-day weight variations were generally unimportant. Some significant differences were found, but they probably depended mainly on the varying numbers of newly arrived, lighter birds in the resting flocks. There was a tendency to slightly lower weights in connection with temperature falls. Again, this may have depended largely on the arrival of leaner and departure of fatter birds and possibly also on the waste of energy of resting birds, which were stimulated to "migratory unrest" activities by the weather change, whether eventually departing or not.

9. Seasonal variations in weight at Ledsjär were negligible. Data obtained from the British Isles indicate a rise in weight during August-October and a maintained large weight (= fat deposition) throughout the winter season. This might be an adaptation to the comparatively hard climatic stresses prevailing on wintering grounds situated farther north, e.g. by forming a prophylactic preparation for the performance of "hard weather flights" during cold spells with frost and scarcity of food. Winter peaks of weight is a well-known phenomenon in passerine species wintering in temperate areas.
10. Recapture weights in juveniles showed an average daily gain of weight after the 3rd day of about 1 gm with extremes at 3 gm a day. Available data on several different smaller-sized passerine migrants indicate an average rise of about 0.4-0.8 gm a day. In adult Dunlins only quite small weight gains which were not significant were recorded, probably because of the very short resting-periods, barely extending over the period of initial weight loss (cf. point 11).
11. Dunlins arriving with appreciable fat stores show a pronounced loss of weight during the first two days, followed by an uninterrupted increase. The leanest birds, on the other hand, show no weight loss at all, but increase steadily from their arrival. Similar results have been obtained from investigations on resting passerines. Possibly, such birds which arrive in a comparatively fat condition are still in a "migratory mood" causing them to waste much time and energy on "migratory unrest" activities, which results in a loss of weight. Gradually the "migratory mood" is weakened so that the birds concentrate more on feeding activities. Birds arriving in a lean condition, however, should be expected to have a much stronger impulse to feed from the beginning.
12. The number of recaptures obtained generally showed a decline with increasing initial weights. Thus larger fat stores indicate a greater readiness to depart. However, there was no support for the assumption that a certain level of fat deposition has to be reached before the birds are able to continue the passage. Adults in July and juveniles in late September seemed ready to depart with very small fat stores of only a few gm.

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