

# STOPOVER LENGTH, BODY MASS AND FUEL DEPOSITION RATE IN AUTUMN MIGRATING ADULT DUNLINS *Calidris alpina*: EVALUATING THE EFFECTS OF MOULTING STATUS AND AGE

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**ABSTRACT** The stopover of adult Dunlins, *Calidris a. alpina* during autumn migration at Ottenby, S.E. Sweden, was investigated. The proportion of Dunlins actively moulting their flight feathers was higher among second-year (2-yr) birds than among older ones (3-yr+). We compared stopover length, arrival body mass, departure body mass and rate of body mass increase between 2-yr and 3-yr+ birds, and between moulting and non-moulting birds, respectively. To estimate length of stopover, a simple mark-recapture model, assuming a constant stopover and capture probability, was fitted to the data on recaptured Dunlins. Maximum likelihood estimates of the daily stopover probability and its variance are provided. Second-year Dunlins made longer stopovers than older ones, but moulting and non-moulting birds did not differ in their stopover length. Rates of body mass change did not differ between age and moult categories. Nor did arrival body mass differ between the four categories. However, 2-yr birds gained more mass before departure than older ones did. Observed stopover length, body mass at ringing and body mass at last recapture were correlated with rate of body mass increase to investigate whether state-dependent decisions were made by the Dunlins. Stopover length appeared to be independent of both body mass at ringing and rate of body mass change in all age and moult categories, indicating that the simplifying assumption of a constant stopover probability in our stopover model was valid. In non-moulting birds, body mass at ringing was negatively related to rate of body mass increase. The results are evaluated in terms of energy-minimised and speed-maximised migration.

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## INTRODUCTION

Many birds perform annual migrations between their breeding and non-breeding sites, thereby optimising the use of seasonal environments (Fretwell 1972, Blem 1980, Alerstam & Högstedt 1982). Energy reserves necessary for these movements are generally stored as fat prior to departure from the breeding grounds in autumn or the wintering grounds in spring (Berthold 1975, Blem 1976), but sometimes non-fat components are stored as well (Lindström & Piersma 1993). For long-distance migrants, energy reserves must be replenished several times at intermediate staging sites along the

migration route. It has been suggested that fat reserves at departure and stopover length are determined by different optimization criteria (Alerstam & Lindström 1990). Thus, it is assumed that a bird "chooses" when to leave a site on the basis of its present fat reserve, rate of fat gain and its expected forthcoming options (Biebach 1985, Alerstam & Lindström 1990).

The nominate subspecies of Dunlin, *Calidris a. alpina*, is a common migrant wader in Europe (e.g. Cramp & Simmons 1983). These birds breed in northern Scandinavia and northern Russia east to the Taimyr Peninsula (Hale 1980, Gromadzka 1989), and winter mainly in Britain, Ireland and

France (Pienkowski & Pienkowski 1983, Gromadzka 1989). Some of these Dunlins stop over at Ottenby, southeast Sweden, during autumn migration (for recoveries of Dunlins ringed at Ottenby see Liljefors *et al.* 1985 and Pettersson *et al.* 1986).

It has been reported that the stopover length of juvenile Dunlins is longer than that of adult ones (Pienkowski & Dick 1975). During autumn migration, juvenile birds pass through Ottenby about 6 weeks later than the adults. As a result, juveniles and adults are exposed to different feeding conditions. Among the adults, two age categories can be distinguished: second calendar year (2-yr) Dunlins which were juveniles the previous year (sometimes these birds are called immature, but we will call both groups adult for convenience) and older Dunlins (3-yr+). These age categories migrate together (Holmgren *et al.* 1993) and hence face the same challenges during migration.

A proportion (20-50%, depending on age) of the adult Dunlins migrating through the Baltic region in autumn are in the process of moulting their wing feathers (Lilja 1969, Stanley 1972, Gromadzka 1986, Holmgren *et al.* 1993). Moulting is an energy-demanding process (Kendeigh 1949, King 1981, Lindström *et al.* in press). Furthermore, the surface of a wing is incomplete if it contains growing wing feathers, which will make flight more expensive. Piersma & Jukema (1993) suggested that only those Bar-tailed Godwits *Limosa lapponica* which were in best condition during spring migration were able to moult body feathers while resting. Hence, moulting birds are expected to have a higher energy expenditure than non-moulting birds.

In practice, the stopover length cannot be measured directly since no birds are caught immediately after arrival and immediately before departure, i.e. observed stopover lengths are always minimum values. Lavee *et al.* (1991) developed a model in which stopover lengths can be estimated. However, their model requires an estimate of the capture probability, which can not be obtained if birds are recaptured only once. To solve this problem, a simple mark-recapture model was developed with which stopover lengths can be estimated independently of capture probability.

The theory of optimal bird migration according to Alerstam & Lindström (1990) suggests that birds on a migration make state-dependent decisions during stopover. One of their predictions is that both fat deposition rate and ringing body mass should be negatively correlated with stopover length. They suggested further that birds maximising speed of migration can be distinguished from birds minimising energy expenditure on migration. In the former case, departure fat load should be correlated with fuel deposition rate, whereas no such correlation would be expected in the latter case. The theory assumes that fat deposition rate remains constant during the stopover.

The aim of this study was to ascertain whether stopover length, fuel (fat and non-fat) deposition rate, and body mass at arrival and departure vary depending on the age and/or moulting status of Dunlins. We also used the data obtained to test the assumptions and the predictions of the energy-minimising and the speed-maximising models of Alerstam & Lindström (1990).

## MATERIAL AND METHODS

### Trapping and processing

Migratory waders were caught in walk-in traps in July-August from 1985 to 1988 at Ottenby, the southernmost point of Öland, an island in south-eastern Sweden (56°, 12'N 16°, 24'E). Approximately 100 traps were used, but the number of traps varied slightly depending on the condition of the floating beds of seaweed. Traps were checked hourly during the daylight period each day. Trapped Dunlins were brought indoors and ringed immediately. They were also weighed to the nearest 0.5 g (body mass at ringing) with a Pesola spring balance. Total head length and length of the left wing were measured to the nearest mm (Svensson 1984). Recaptured Dunlins were reweighed. The body mass at last recapture is referred to as the recapture body mass. Rate of body mass change was calculated by dividing the difference in body mass between recapture and ringing by the time that had elapsed in between. For a more detailed description

of the wader ringing scheme at Ottenby, see Blomqvist *et al.* (1987).

### Age and moult categories

The 2-yr Dunlins were identified on the basis of the remaining juvenile, inner median coverts (Prater *et al.* 1977), which were distinguished from adult buff coverts. The adult buff coverts are rectangular and have a blackish center sharply delimited by the rich chestnut fringe. Juvenile coverts are rounded and have a brownish center; with the colour gradually turning yellowish towards the fringe (Clark 1984, Gromadzka 1985, 1986). Nearly all Dunlins could be aged based on this feather characteristics, except 10 specimens that were in such an advanced moulting stage that they had already grown new inner median coverts. Dunlins that had one or more incompletely formed wing feathers were classified as moulting. Those with a complete wing feather set were classified as non-moulting irrespective of whether all feathers were old or some were newly formed and of full length.

### Estimate of stopover probability

Normally, the stopover length of a bird is conservatively measured as the time elapsed between ringing and last recapture (here referred to as the observed stopover length). If the bird is not captured immediately after arrival or not recaptured immediately prior to departure, then the observed stopover length will be shorter than the real one. To estimate true stopover lengths, a mark-recapture model essentially following Jolly (1965) and Seber (1973) was developed.

For the sake of simplicity, we assumed that each individual had a constant probability ( $s$ ) of staying for one unit of time ( $t$ ). Furthermore, we assumed that capture probability was unaffected by any previous capture of the same bird. The probability of recapturing a bird  $t$  time units after it has been ringed can be described as:

$$p(t) = s^t c,$$

i.e. the probability of staying  $t$  time units is the probability of staying one time unit ( $s$ ) raised to  $t$ . We ignore whether or not the bird is caught during this

period, but it must be caught at time unit  $t$ , the probability of which is  $c$  (i.e. the time-unit-specific capture probability of a bird present). Thereafter, the bird stays without being caught  $(1-c)$  an unknown number of time units ( $u$ ) before it leaves  $(1-s)$ . Hence, the probability of a bird being recaptured after  $t$  time units and then staying another  $u$  time units before it leaves is:

$$P(t, u) = s^t c [s(1-c)]^u (1-s). \quad (1)$$

The number of time units a bird stays after the last recapture is unknown. By summing the probabilities for all possible values of  $u$  (zero to infinity), we get the probability of a bird being recaptured  $t$  time units after it was ringed, irrespective of the length of the stay afterwards:

$$P(t) = \sum_{u=0}^{\infty} P(t, u) = \frac{s^t c (1-s)}{1-s+s c}. \quad (2)$$

It is of interest to get an expression for the probability of recapturing a bird  $t$  time units after ringing, given that it belongs to a data set consisting of  $n$  recaptured birds. In this way, the stopover probability can be estimated independently of the capture probability. Let  $t_{\min}$  be the shortest possible stopover length (not the shortest obtained, normally  $t_{\min} = 1$ ) in the data set. The probability of an observed stopover length being at least  $t_{\min}$  long, equals the sum of the recapture probabilities from  $t_{\min}$  to infinity:

$$P(\text{data}) = \sum_{t=t_{\min}}^{\infty} P(t) = \frac{s^{t_{\min}} c}{1-s+s c}. \quad (3)$$

The probability that a bird in the data set has an observed stopover length  $t$  is calculated by dividing (2) by (3):

$$P(t | \text{data}) = s^{t-t_{\min}} (1-s). \quad (4)$$

The value of the unknown parameter  $s$  and its variance can now be estimated by the maximum

likelihood method (Fisher 1922, 1925, Seber 1982). Let  $L$  be the likelihood function of the observed data set. For a set of  $n$  birds with the observed stopover length  $t_i$  ( $i = 1..n$ )

$$L = \prod_{i=1}^n s^{t_i - t_{\min}} (1-s).$$

The derivative

$$\frac{\partial \log L}{\partial s} = -\frac{n}{1-s} - \frac{n t_{\min}}{s} + \frac{1}{s} \sum_{i=1}^n t_i = 0$$

is solved with respect to  $s$  to get the maximum likelihood estimate of the stopover probability ( $\hat{s}$ ). Hence,

$$\hat{s} = \frac{\bar{t} - t_{\min}}{1 + \bar{t} - t_{\min}}, \quad (5)$$

where  $\bar{t}$  is the arithmetic mean stopover length in the data set. The variance of the estimate is found by solving

$$\frac{\partial^2 \log L}{\partial s^2} = \frac{n}{(1-\hat{s})^2} + \frac{n(\bar{t} - t_{\min})}{\hat{s}^2} = -\frac{1}{\text{var}(\hat{s})} \quad (6)$$

using the estimated  $s$ -value.

To estimate the mean stopover length of all birds making stopovers, an arithmetic mean is calculated by considering the proportional contribution of each value to the total data set. The estimate of the mean stopover length in the population

$$\tau = \sum_{i=1}^n \hat{s}^i (1-\hat{s}) t = \frac{\sum_{i=1}^n \hat{s}^i t}{1-\hat{s}} = \bar{t} - t_{\min} \quad (7)$$

after substituting (5) for  $\hat{s}$ .

Differences in stopover probabilities were tested pairwise between categories by calculating values of  $d$ , the standard normal deviate. When comparing two categories

$$d = \frac{\hat{s}_1 - \hat{s}_2}{\sqrt{\text{var}(\hat{s}_1) + \text{var}(\hat{s}_2)}}.$$

In the ringing scheme at Ottenby, individuals trapped a second time on the same day are not registered, and this is also the case for the present data. The longest possible observed stopover that could have fit within a day is 20 h this time of the year. As a consequence, Dunlins ringed in the evening and recaptured within 20 h the day after were not used in the estimation of stopover time. Hence,  $t_{\min}$  is 21 h in this study.

## Statistics

Most of the Dunlins observed passed through Ottenby during a rather short period; i.e. 45 to 72% were caught within a period of 5 days during each of the given years. Mean capture dates did not differ by more than 13 days between the years studied (Holmgren *et al.* 1993). Annual effects were therefore considered negligible, and data from the four years were pooled. The theory of optimal bird migration sensu Alerstam & Lindström (1990) only makes predictions about fat gain during the stopover. Therefore, Dunlins not gaining body mass were excluded from the correlation analyses. One 3-yr+ Dunlin was judged to be a statistical outlier because of its extremely long stopover length (106 h) and high body mass at ringing (65 g), and was therefore excluded from the analyses. Statistics follow Sokal & Rohlf (1981) and the SYSTAT, Inc. statistical package (1991).

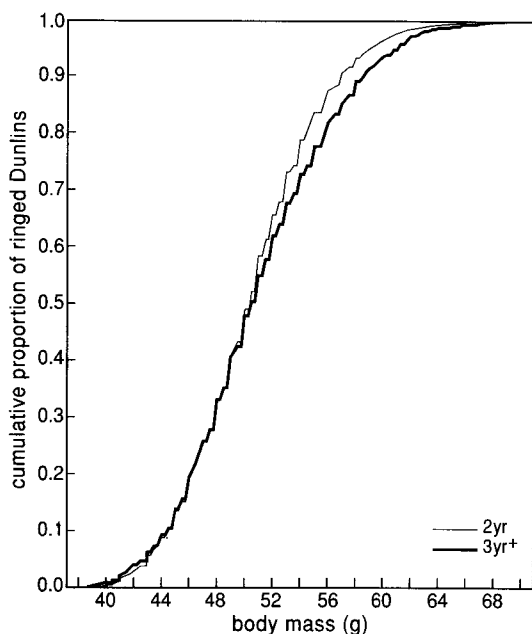
## RESULTS

### Stopover lengths

Maximum observed stopover lengths ranged from 2.6 to 9.1 days between age and moult categories, with the longer stopovers predominantly occurring in 2-yr Dunlins. The probability of staying ( $s$ ) was significantly higher in 2-yr birds than in 3-yr+ birds (Table 1;  $d = 4.76$ ,  $p < 0.001$  among non-moulting and  $d = 3.39$ ,  $p < 0.001$  among moulting birds). Moulting status had no effect on

**Table 1.** Observed mean stopover length of Dunlins recaptured more than 20 h after ringing ( $\bar{t}$ ). Mean stopover length of Dunlins in the population ( $\tau$ ); daily stopover probability  $\hat{s}$  and its standard deviation are estimated according to equations 5,6 and 7. The Dunlins are classified according to age and moulting status. Data are pooled over the years 1985-88.

Age	Moulting status	Observations		Estimates		
		$\bar{t}$ (days)	$N$	$\tau$ (days)	$\hat{s}$ (day <sup>-1</sup> )	$\hat{\sigma}$
2-yr	Inactive	2.31	28	1.44	0.50	0.06
"	Active	2.80	29	1.93	0.60	0.05
3-yr+	Inactive	1.43	48	0.55	0.18	0.03
"	Active	1.59	11	0.72	0.26	0.08



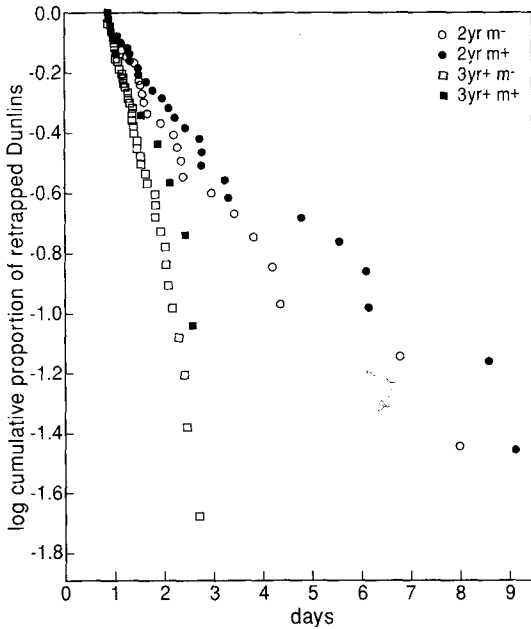
**Fig. 1.** Logarithm of cumulative proportion of recaptured Dunlins versus time between ringing and last recapture of Dunlins (classified according to age and moulting status) recaptured within the same year as they were ringed at Ottenby, 1985-88. Only individuals with more than 20 h elapsed between ringing and last recapture are included. Proportion of recaptured birds with an observed stopover length exceeding  $t'$  can be calculated by summing eq.4 from  $t=t'$  to infinity. Data are presented to conform to the logarithm of this proportion over  $t'$  (in days). A linear relationship is expected, with the slope equal to the logarithm of the daily stopover probability.

stopover probability ( $d = 1.17$ ,  $p > 0.05$  among 2-yr and  $d = 0.90$ ,  $p > 0.05$  among 3-yr+ birds). Fig.1 shows the logarithm of the cumulated data, where the slopes indicate the logarithm of the stopover probability. Pooling the moulting and non-moulting Dunlins within each age group generated the estimate of the mean stopover length of 1.7 days for 2-yr birds and 0.6 days for 3-yr+ birds.

The 2-yr birds made up 29% of the adult Dunlins ringed in the 4-year study. Since 2-yr Dunlins made longer stopovers than 3-yr+ birds, it is likely that the catch of 2-yr birds are represented in a higher proportion of the total catch than would be expected based on their frequency in the population. Of the ringed Dunlins estimated to stay more than 20 h, 5.2-7.0% (6.3%, total average) were recaptured. Among these recaptured birds, no significant differences were found between ages or between moult categories ( $p > 0.05$ , pairwise G-test). This suggests that although 3-yr+ birds make shorter stopovers, they are more apt to be recaptured during this period compared with 2-yr birds. Thus, it seems that the proportion of 2-yr Dunlins ringed is, after all, an accurate estimate of the proportion in the migrating population.

### Body masses

Body masses of the Dunlins ranged from 35 to 74 g. Mean body masses were close to 51 g for all categories (Table 2). Nevertheless, 2-yr birds, on average, weighed slightly more than 3-yr+ birds



**Fig. 2.** Frequency of body masses at ringing expressed as the cumulative proportion in 2-yr ( $N=1582$ ) and 3-yr+ ( $N=3897$ ) Dunlins respectively.

( $F_{1,5475} = 8.21, p = 0.004$ , two-way-ANOVA). By pooling moulting and non-moulting Dunlins of each age, we found that the cumulative distribution of body masses differed among birds in the upper-50% range, with 2-yr birds being significantly heavier than 3-yr+ birds ( $p < 0.001$ , Kolmogorov-Smirnov two sample test). Among the lower 50%, the body mass distributions were similar (Fig.2).

**Changes in body mass**

Although most of the recaptured Dunlins gained body mass, 12 out of 115 (10%) showed a loss. The average gain was 1.8-2.7 g/day (Table 2). Since there was a negative relationship between body mass at ringing and rate of body mass change (see below), differences in the rate of body mass change were tested in an ANCOVA correcting for body mass at ringing. Moulting and non-moulting birds did not differ in their rate of body mass change (Table 2;  $F_{1,111} = 1.32, p > 0.05$ , two-way ANCOVA). Nor was there a difference in rate of body mass change related to age ( $F_{1,111} = 1.55, p > 0.05$ ). However, 3-yr+ birds showed a higher variance (5.51) in rate of body mass change than 2-yr birds (2.35;  $F_{56,59} = 2.34, p = 0.001$ ). Among the 50% of the Dunlins within each age and moult category which showed the highest rate of body mass change, 3-yr+ birds had a higher rate of body mass change (3.9 g/day) than 2-yr birds (3.2 g/day;  $F_{1,53} = 7.886, p = 0.007$ ) but here again, there was no effect of moult ( $F_{1,53} = 2.337, p > 0.05$ ). Dunlins that increased their body mass faster than 3 g/day are listed in the Appendix.

**Relationships between stopover parameters**

If it is assumed that changes in body mass correspond to changes in fat deposits and that body mass at recapture corresponds to departure fat load, then the positive correlations between rate of mass gain and recapture body mass in all categories of Dunlins, except non-moulting, 2-yr birds, support the hypothesis that they are maximising speed of

**Table 2.** Statistics on body masses of ringed adult Dunlins and on rate of change in body mass of Dunlins recaptured more than 20 h after they had been ringed. The Dunlins are classified according to age and moulting status but pooled over the years 1985-88.

Age	Moulting status	Body mass (g)				Rate of body mass change (g/day)			
		Mean	SD	range	N	Mean	SD	range	N
2-yr	Inactive	51.1	5.5	35.0 - 71.0	838	1.8	1.6	-1.50 - 5.76	28
"	Active	51.3	5.6	39.0 - 70.0	749	2.0	1.5	0.00 - 5.14	29
3-yr+	Inactive	50.6	4.9	37.5 - 74.0	3224	2.1	2.3	-4.00 - 7.30	48
"	Active	50.8	4.8	37.0 - 66.0	695	2.7	2.5	-2.85 - 5.76	11

**Table 3.** Results of partial correlations between the three parameters (pairwise, the third parameter held constant) body mass at ringing ( $M1$ ), rate of body mass change ( $MC$ ) and observed stopover length ( $T$ ). Results of partial correlation between body mass at last recapture ( $M2$ ) and rate of body mass change, with body mass at ringing held constant. Correlations are made within age and moult categories; only Dunlins that had gained body mass were included in the analysis.

Age	Moulting status	$M1 \cdot T$		$M1 \cdot MC$		$MC \cdot T$		$MC \cdot M2$		<i>df</i>
		<i>r</i>	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>	<i>t</i>	<i>r</i>	<i>t</i>	
2-yr	Inactive	0.10	0.47	-0.46	2.34*	-0.18	0.80	0.28	1.31	20
"	Active	0.11	0.51	-0.11	0.52	-0.17	0.81	0.42	2.17*	22
3-yr+	Inactive	-0.30	1.80	-0.35	2.19*	-0.25	1.50	0.81	8.07**	34
"	Active	-0.16	0.42	-0.09	0.25	-0.24	0.64	0.70	2.59*	7

\*  $p < 0.05$ , \*\*  $p < 0.001$ . Other cases are not significant,  $p > 0.05$

migration (Table 3). However, contrary to expectation, body mass at ringing and fat deposition rate were not negatively correlated with the observed stopover length for any of the four categories (Table 3). Nor did the birds show a constant fat deposition rate. Among non-moulting birds, those with a low body mass at ringing generally showed a high rate of body mass change (Table 3). This could have been the result of the fat deposition rate levelling off as the amount of fat reserves increased. Alternatively, fat deposition might have been interrupted once a critical fat load was reached. However, such a strategy would not be expected for speed-maximising migrants.

## DISCUSSION

### Stopover length

In this study we reported that 2-yr Dunlins tended to stay longer than 3-yr+ Dunlins, but that the flight-feather moulting status had no effect on stopover length. Pienkowski & Dick (1975) found a difference in stopover length between adult (2-yr+; maximum observed: 4 days) and juvenile Dunlins (1-yr; maximum observed: 16 days) on autumn migration in Morocco. The longest stopover observed in our study was 4 days for 3-yr+ birds and 9 days for 2-yr birds; which is longer than that reported from Morocco where 2-yr and 3-yr+ Dun-

lins were not distinguished. On the spring passage in Morocco, however, mean stopover length was 11 days in 1982 and 16 days in 1981 (Piersma 1987), which greatly exceeds our estimated mean stopover lengths, ranging from 0.6 to 1.9 days. An estimate of stopover length comparable to ours was reported by Butler *et al.* (1987) for the Western Sandpiper, *C. mauri*, during autumn migration along the west coast of North America. The assumptions they used in their model were the same as ours, and their estimated daily probability of staying was 0.41 for all adults, which falls between our values of 0.19 for 3-yr+ and 0.56 for 2-yr Dunlins. Although this is the first study to report such a difference between 2-yr and 3-yr+ birds, it might reflect a tendency for younger birds to stay longer than older birds. However, in a study on the stopover length of the Semipalmated Sandpiper *C. pusilla*, Dunn *et al.* (1988) found no difference between adults and juveniles.

### Rate of change in body mass

Flight feather moulting status had no effect on the rate of change in body mass. Nor was it correlated with body mass at ringing or recapture. Hence, moulting did not seem to be an important source of energetic stress in the Dunlins. However, the moult in these Dunlins is much less intense than that occurring in stationary birds at ordinary moulting sites (Holmgren *et al.* 1993). The two age cate-

gories of Dunlins gained mass at a similar rate. Maximum values, however, were much higher in 3-yr+ Dunlins than in 2-yr birds, suggesting that the capacity for body mass change is higher in the older Dunlins.

Our observed mean rate of body mass increase ranged between 1.8 and 2.7 g/day. Average rates of increase in body mass reported from other studies on Dunlins are 1.2 and 1.6 g/day (in different years, Morocco; Piersma 1987), 1 g/day (E. Sweden; Mascher 1966), 0.5 g/day (the Wash, England; Pienkowski *et al.* 1979) and 1.1 g/day (England; Eades & Okill 1977). Also, maximum rates of body mass gain (5.1 to 7.3 g/day) observed are higher than those found in the literature, i.e. 3 g/day (E. Sweden; Mascher 1966), 0.9 g/day (the Dutch Wadden Sea; Goede *et al.* 1990) and an average maximum of 1.6 g/day (England; Eades & Okill 1977). Based on a calculated, maximum daily metabolizable energy intake (Kirkwood 1983), Lindström (1991) estimated maximum fat deposition rates in birds. The rate for a Dunlin with a lean body mass of 46 g would be 2.5 g/day. In the light of previous findings and theoretical predictions, the rates of body mass increase in our study are high. However, the increase in body mass may not be due entirely to fat deposition. For instance, in the premigratory phase, body mass increase may also be due to an increase in muscle mass (Piersma & Jukema 1990, Lindström & Piersma 1993) which contains less energy per unit mass, and therefore can be deposited at a higher rate than fat. During the migratory phase, however, flight muscles ought to be fully developed and protein storage should be less pronounced than during the premigratory phase. Second, the birds may be dehydrated upon arrival at a stopover site. However, a sample of juvenile Dunlins showed that a constant proportion of the fat-free body mass consisted of water irrespective of fat content (Mascher & Marcström 1976). Third, there is no doubt that soon after arrival birds fill up their empty digestive tract. Before departure from a staging site, Knots, *C. canutus*, and probably other species, empty their digestive tract (Swennen 1992). Thus gained body mass could partly consist of undigested matter. None of the alternatives can

be excluded on the basis of present knowledge, and perhaps all contribute partially to explaining the high rates of body mass increase.

#### Time- or energy-minimised migration?

The correlations between body mass at recapture and rate of body mass increase suggest, at least at first glance, that the Dunlins are trying to maximise their speed of migration *sensu* Alerstam & Lindström (1990). However, the fact that neither body mass at ringing nor rate of body mass increase was correlated with stopover length raises some doubts. If the migrants commonly wait for suitable weather conditions and weather conditions vary in an unpredictable way then stopover length would appear to be random, and consequently, body mass at ringing and rate of body mass change would be poor predictors of stopover length. A random stopover model fitted well with observations of small birds crossing the Sahara (Lavee *et al.* 1991), autumn migrating Western Sandpipers (Butler *et al.* 1987) and of the Dunlins in this study. Body mass at ringing did not predict stopover length in any of these studies. This lack of correlation was also found by Dunn *et al.* (1988) and Page & Middleton (1972) when studying Semipalmated Sandpipers. Interestingly, though, Mascher (1966) claims that autumn migrating Dunlins in central Sweden carrying a large amount of fat stay shorter periods than their leaner conspecifics. By contrast, in passerines it seems more common for lean migrants to stay longer than fat ones (Cherry 1982, Bairlein 1985, Biebach 1985, Pettersson & Hasselquist 1985, Biebach *et al.* 1986, Moore & Kerlinger 1987, Safriel & Lavee 1988, Loria & Moore 1990).

Alerstam & Lindström (1990) assumed a constant fat deposition rate, and did not predict a negative correlation between body mass at ringing and rate of body mass increase like we have found (Table 3). It might, nevertheless, be possible to explain the correlation in terms of optimal bird migration if the assumptions are changed. When weather conditions are unsuitable, speed-maximising migrants can be expected to continue to deposit fat, and thereby also continue to gain potential flight distance. In contrast, energy-minimising migrants



- Dunn, P.O., T.A. May & M.A. McCollough 1988. Length of stay and fat content of migrant semipalmated sandpipers in Eastern Maine. *Condor* 90:824-835.
- Eades, R.A. & J.D. Okill 1977. Weight changes of Dunlins at the Dee Estuary in May. *Bird Study* 24:62-63.
- Fischer, R.A. 1922. On the mathematical foundation of theoretical statistics. *Philos. Trans. R. Soc. Lond. A Math. Phys. Sci.* 222:309-368.
- Fischer, R.A. 1925. Theory of statistical estimation. *Proc. Cambr. Philos. Soc.* 22:700-725.
- Fretwell, S.D. 1972. Populations in a seasonal environment. *Monogr. Popul. Biol.* 5. Princeton university press, Princeton.
- Goede, A.A.E., Nieboer & P.M. Zegers 1990. Body mass increase, migration pattern and breeding grounds of Dunlins, *Calidris alpina*, staging in the Dutch Wadden Sea in spring. *Ardea* 78:135-144.
- Gromadzka, J. 1985. Further observations on the wing plumage of Dunlins. *Wader Study Group Bull.* 4:32-33.
- Gromadzka, J. 1986. Primary moult of adult Dunlins *Calidris alpina* of different age during autumn migration. In: C. Hjort, J. Karlsson & S. Svensson (eds) *Baltic Birds IV, Vår Fågelvärld Suppl.* 11: 51-56. Sveriges Ornitologiska Förening, Stockholm.
- Gromadzka, J. 1989. Breeding and wintering areas of Dunlin migrating through southern Baltic. *Ornis Scand.* 20:132-144.
- Hale, W.G. 1980. Waders. *The New Naturalist* 65. Collins, London.
- Holmgren, N., H. Ellegren & J. Pettersson 1993. The adaptation of moult pattern in migratory Dunlins *Calidris alpina*. *Ornis Scand.* 24:21-27.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225-247.
- Kendeigh, S.C. 1949. Effect of temperature and season on the energy resources of the English sparrow. *Auk* 66:113-127.
- King, J.R. 1981. Energetics of avian moult. *Proc. XVII Int. Orn. Congr.* 312-317.
- Kirkwood, J.K. 1983. A limit to metabolizable energy intake in mammals and birds. *Comp. Biochem. Physiol.* 75A:1-3.
- Kuenzi, A.J., F.R. Moore & T.R. Simons. 1991. Stopover of Neotropical landbird migrants on East Ship Island following trans-gulf migration. *Condor* 93: 869-883.
- Lavee, D., U.N. Safriel & I. Meilijson 1991. For how long do trans-Saharan migrants stop over at an oasis? *Ornis Scand.* 22:33-44.
- Lilja, I. 1969. On the postnuptial wing moult of migratory Dunlin *Calidris alpina*. *Ann. Repr. Orn. Soc., Pori*:40-43.
- Liljefors, M., J. Pettersson & T. Bengtsson 1985. Recruitment areas for migrants trapped at Ottenby Bird Observatory. Special report from Ottenby Bird Observatory No. 5. Ottenby Fågelstation, Degerhamn.
- Lindström, Å. & T. Alerstam 1992. Optimal fat loads in migrating birds: a test of the time minimisation hypothesis. *Am. Nat.* 140:477-491.
- Lindström, Å. & T. Piersma 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* 135:70-78.
- Lindström, Å., G.H. Visser & S. Daan. The energetic cost of feather production is proportional to basal metabolic rate. *Physiol. Zool.* in press.
- Lindström, Å., D. Hasselquist, S. Bensch & M. Grahm. 1990. Asymmetric contests over resources for survival and migration: a field experiment with Blue-throats. *Anim. Behav.* 40:453-461.
- Lindström, Å. 1991. Maximum fat deposition rates in migrating birds. *Ornis Scand.* 22:12-19.
- Loria, D.E. & F.R. Moore 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behav. Ecol.* 1:24-35.
- Mascher, J.W. 1966. Weight variations in resting Dunlins *Calidris a. alpina* on autumn migration in Sweden. *Bird-Banding* 37:1-34.
- Mascher, J.W. & V. Marcström 1976. Measures, weights and lipid levels in migrating Dunlins *Calidris a. alpina* L. at the Ottenby Bird Observatory, South Sweden. *Ornis Scand.* 7:49-59.
- Moore, F. & P. Kerlinger 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47-54.
- Page, G. & A.L.A. Middleton 1972. Fat deposition in autumn migration in the Semipalmated sandpiper. *Bird-Banding* 43:85-96.
- Pettersson, J. & D. Hasselquist 1985. Fat deposition and migration capacity of Robins *Erithacus rubecula* and Goldcrest *Regulus regulus* at Ottenby, Sweden. *Ring. & Migr.* 6:66-75.
- Pettersson, J., A. Sandström & K. Johansson 1986. Wintering areas of migrants trapped at Ottenby Bird Observatory. Special report from Ottenby Bird Observatory No. 6. Ottenby Fågelstation, Degerhamn.
- Pienkowski, M.W. & W.J.A. Dick 1975. The migration and wintering of Dunlin *Calidris alpina* in north-west Africa. *Ornis Scand.* 6:151-167.
- Pienkowski, M.W., C.S. Lloyd & C.D.T. Minton 1979. Seasonal and migrational weight changes in Dunlins. *Bird Study* 26:134-148.
- Pienkowski, M.W. & A.E. Pienkowski 1983. WSG project on the movements of wader populations in western Europe: eighth progress report. *Wader Study Group Bull.* 38:13-22.
- Piersma, T. & J. Jukema 1990. Budgeting the flight of a long-distant migrant: changes in nutrient reserve

- levels of Bar-tailed Godwits at successive spring staging sites. *Ardea* 78:315-337.
- Piersma, T. 1987. Hop, skip or jump? Constraints on migration of arctic waders by feeding, fattening and flight speed. *Limosa* 60:185-194.
- Piersma, T. & J. Jukema 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the Bar-tailed Godwit. *Condor* 95:163-177.
- Prater, A.J., J.H. Marchant & J. Vourinen 1977. Guide to the identification and ageing of Holarctic waders. BTO Guide 17. BTO, Tring.
- Rappole, J.H. & D.W. Warner 1976. Relationships between behaviour, physiology and weather in avian transients at a migration stopover site. *Oecologia* 26:193-212.
- Safriel, U.N. & D. Lavee 1988. Weight changes of cross-desert migrants at an oasis - do energetic considerations alone determine the length of stopover. *Oecologia* 76:611-619.
- Seber, G.A.F. 1973. The estimation of animal abundance and related parameters. Griffin, London.
- Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. Macmillan, London.
- Sokal, R.R. & F.J. Rohlf 1981. Biometry. Freeman & Co., New York.
- Stanley, P. 1972. The WWRG visit to Denmark & Sweden, Aug 1972, New information on the timing of Dunlin wing moult. *Wader Study Group Bull.* 7:9-10.
- Svensson, L. 1984. Identification guide to European passerines. Lars Svensson, Stockholm.
- Swennen, C. 1992. Observations on the departure of Knots from the Dutch Wadden Sea in spring. *Wader Study Group Bull.* 64, Suppl:87-90.
- van het eiland Öland in Zweden. De vogels werden daar gevangen en geringd. Verder onderzocht men de mate van rui en bepaalde het lichaamsgewicht. Zij vergeleken vier categorieën: vogels in hun tweede jaar en oudere vogels, en voor beide leeftijdsgroepen de mate van slagpennenrui. Onder de tweedejaars waren er meer actief ruiend dan onder de ouderen.

De duur van de pleisterperiode werd geschat met behulp van een toevalsmodel en op grond van de terugvangkans (Fig. 1). Deze periode bleek te variëren tussen enkele dagen en ruim een week. De tweedejaars bleken langer te pleisteren dan de ouderen, maar tussen ruiende en niet ruiende vogels van dezelfde leeftijd was geen aantoonbaar verschil in pleisterduur (Tabel 1).

Het gemiddelde gewicht van de tweedejaars lag iets hoger dan dat van de ouderen (Fig. 2). Tussen de vier categorieën was echter geen duidelijk verschil in aankomstgewicht en ook niet in de snelheid waarmee het gewicht toenam tijdens het pleisteren (Tabel 2). Het gemiddelde gewichtsverschil tussen de leeftijdsgroepen wordt dan ook veroorzaakt door de langere verblijfsduur van de tweedejaars vogels: hun vertrekgewicht is hoger.

Op grond van het ontbreken van duidelijke correlaties wordt gesuggereerd dat de beslissing om het pleistergebied weer te verlaten onafhankelijk is van aankomstgewicht en de snelheid van de gewichtstoename (Tabel 3). Verder blijkt bij niet ruiende vogels een negatief verband te bestaan tussen het lichaamsgewicht bij het ringen en de snelheid van de gewichtstoename. Dit houdt in dat als ze met een laag gewicht aankomen, de reserves sneller worden aangevuld. Deze resultaten sluiten goed aan bij de hypothese dat bij de trek de energetische kosten zo laag mogelijk worden gehouden en de snelheid zo hoog mogelijk.

## SAMENVATTING

Dit onderzoek gaat over Bonte strandlopers die tijdens hun herfsttrek pleisteren bij Ottenby, de zuidelijke punt

## APPENDIX

Recaptured adult Dunlins with an average rate of body mass change above 3 g/day. Body mass at ringing, recapture body mass (i.e. at last recapture) and observed stopover length (i.e. between ringing and last recapture) are presented.

Mass change (g/day)	Body mass at		Observed stopover length (h)	Age	Moulting status (* = active)
	ringing (g)	recapture (g)			
7.3	42.5	49.5	23	3-yr+	
7.1	45.0	55.0	34	3-yr+	
5.8	48.5	54.5	25	2-yr	*
5.8	48.5	54.5	25	3-yr+	*
5.6	50.0	57.0	30	3-yr+	
5.1	43.0	49.0	28	2-yr	*
5.1	53.0	67.0	66	2-yr	*
5.0	48.0	54.0	29	3-yr+	
4.9	49.5	54.0	22	3-yr+	*
4.7	52.5	57.0	23	3-yr+	
4.7	43.0	50.0	36	3-yr+	*
4.5	49.0	56.0	37	3-yr+	
4.4	53.0	62.0	49	3-yr+	*
4.3	45.0	49.5	25	3-yr+	
4.2	54.5	61.0	37	3-yr+	*
4.2	49.0	53.5	26	3-yr+	
4.0	45.5	54.0	51	2-yr	*
3.8	49.0	57.5	53	2-yr	*
3.8	45.5	49.0	22	2-yr	
3.8	45.0	52.0	44	3-yr+	
3.8	53.0	58.0	32	2-yr	*
3.7	55.0	62.0	45	3-yr+	*
3.7	51.0	55.0	26	2-yr	*
3.7	51.5	55.0	23	3-yr+	
3.4	43.0	48.0	35	2-yr	
3.4	44.5	47.5	21	3-yr+	*
3.4	43.0	47.0	28	2-yr	
3.4	51.0	62.0	78	2-yr	*
3.4	48.0	52.5	32	2-yr	*
3.3	48.5	68.5	147	2-yr	*
3.2	44.0	49.0	37	3-yr+	
3.2	51.0	60.0	67	2-yr	*
3.1	51.5	59.0	58	3-yr+	
3.1	45.0	53.0	62	3-yr+	*

ERRATUM

In: HOLMGREN et al. 1993. STOPOVER LENGTH, BODY MASS AND FUEL DEPOSITION RATE IN AUTUMN MIGRATING ADULT DUNLINS *Calidris alpina*: EVALUATING THE EFFECTS OF MOULTING STATUS AND AGE - ARDEA 81: 9-20.

Please note that Figures 1 and 2 have been switched (captions are correct).