



The Adaptation of Moulting Pattern in Migratory Dunlins *Calidris alpina*

Noél Holmgren; Hans Ellegren; Jan Pettersson

Ornis Scandinavica, Vol. 24, No. 1. (Jan. - Mar., 1993), pp. 21-27.

Stable URL:

<http://links.jstor.org/sici?sici=0030-5693%28199301%2F03%2924%3A1%3C21%3ATAOMPI%3E2.0.CO%3B2-3>

Ornis Scandinavica is currently published by Nordic Society Oikos.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/oikos.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

The adaptation of moult pattern in migratory Dunlins *Calidris alpina*

Noél Holmgren, Hans Ellegren and Jan Pettersson

Holmgren, N., Ellegren, H. and Pettersson, J. 1993. The adaptation of moult pattern in migratory Dunlins *Calidris alpina*. – *Ornis Scand.* 24: 21–27.

The post-nuptial primary moult of adult (2-year-birds included) Dunlins was investigated along the Baltic coast at Ottenby and Falsterbo, S. Sweden. These birds are on migration and only make short stopovers. During the years 1985–1988 at Ottenby, the proportions of moulting birds varied between 27% and 61%, probably due to annual variations in the timing of their passage. Compared with the older birds, 2-year-birds had more often initiated their moult and, on average, appeared in a more advanced stage of moult. Most of the Dunlins that had initiated moult were actively moulting – some feathers were not of full length and were found growing in a sample of caged individuals.

The raggedness value (i.e. the gap due to not fully grown feathers) generally decreased in later stages of moult. By comparing raggedness values at given stages of moult, migrating Baltic birds generally had smaller gaps than non-migrating English conspecifics. Large gaps were correlated with lower body masses. The adaptive significance of commencing the moult prior to the arrival on moulting grounds and of moult during migration are discussed.

Noél Holmgren, Dept. of Ecology, Theoretical Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden. Hans Ellegren, Dept. of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Box 7055, S-750 07 Uppsala, Sweden. Jan Pettersson, Ottenby Bird Observatory, Pl. 1500, S-380 65 Degerhamn, Sweden.

The nominate subspecies of the Dunlin *Calidris a. alpina* is one of the most numerous waders in the western Palearctic, with breeding areas ranging from northern Fenno-Scandia eastwards at least to the Jenisey river in Russia. The majority of the Dunlins migrating and wintering in western Europe belong to this subspecies (Cramp and Simmons 1983). Additionally, some birds reaching western Europe during migration seem to originate from as far east as the Taimyr peninsula (see Liljefors et al. 1985, Gromadzka 1989, Goede et al. 1990). While Dunlins breeding east of the Ural mountains moult during breeding (Greenwood 1983), most of the Dunlins reaching Europe perform their complete moult after breeding (e.g. Ginn and Melville 1983). A majority of these birds moult in the Wadden Sea area (Denmark, Germany and The Netherlands; Boere 1977, Boere and Smit 1981) and along the coasts of Great Britain (e.g. at the Wash, Hale 1980). After the completion of moult, they may continue to their nearby

wintering areas in Britain, Ireland and France (Pienkowski and Pienkowski 1983).

Dunlins migrating through the Baltic basin have, however, been found to have started their wing moult. This was first observed by Lilja (1969) who recognized that some 20% of the birds passing through Finland were in active wing moult and another 5% in suspended moult. Similarly, during a visit to Ottenby, S.E. Sweden, Stanley (1972) observed that 32% of the Dunlins were in active wing moult and that 12% had suspended moult. More recently, Gromadzka (1986) has documented the moult in Dunlins on the coast of Poland. Here, 56% had started their wing moult and there was a higher proportion moulting among second-year than older birds.

The latter observations are quite surprising since energy demanding processes like moult and migration generally tend not to overlap (Kendeigh 1949, Farner 1964, Stresemann 1967, Payne 1972, Hale 1980). In

Table 1. Number of adult Dunlins ringed during autumn migration at two stopover sites in S. Sweden. The proportions of 2y birds and the proportions of moulting birds of different age categories are indicated.

Site	Year	% 2y	% moulting			N
			3y+	2y	Total	
Ottenby	1985	25.8	27.2	79.2	40.6	1562
Ottenby	1986	39.3	8.4	55.4	26.9	1443
Ottenby	1987	18.8	55.4	87.6	61.4	1032
Ottenby	1988	30.9	24.3	84.4	42.8	1186
Falsterbo	1988	27.3	26.6	89.9	43.9	362

order to explore the significance of the simultaneous migration and moult events, we studied Dunlins migrating through southern Sweden. Our primary aim was to investigate whether the moult pattern of migratory Dunlins deviated from that prevailing in the ordinary moulting areas. Secondly, we wanted to study the influence of a decreased wing area due to moult on migrational energy reserves.

Material and methods

Waders were caught in walk-in-traps in the summers of 1985–1988 at Ottenby, the southernmost point of Öland, S.E. Sweden (56°12'N, 16°24'E). About 100 traps were put on the thick floating beds of seaweed near the shore (see Blomqvist et al. 1987 for details). In 1988, Dunlins were also trapped at Falsterbo, the southwesternmost point of Sweden (55°23'N, 12°50'E). About 25 walk-in traps were used in the shore line both on stranded aggregations of seaweed and directly on the sand. At both sites, the traps were checked once every hour, and trapped birds were processed immediately. Dunlins were ringed, weighed with a Pesola spring balance to the nearest 0.5 g and measured in two ways: total head length to the nearest mm and length of the left wing to the nearest mm (Svensson 1984, method 2).

Each primary and secondary was scored 0–5 points according to Ashmole (1962; see also Ginn and Melville 1983); that is old feathers scored 0, new full-grown feathers scored 5, and growing feathers scored from 1 (a pin only) to 4 (a nearly full-grown one with remaining waxy sheaths). To census the gap in the wing, i.e. the raggedness (see e.g. Haukioja 1971), the score of each growing feather was subtracted from the score of a full grown feather (5) and these scores summed. For example, a bird with two growing feathers of score 1 and 3 respectively, has a raggedness of $(5-1)+(5-3)=6$. A high raggedness score normally refers to a large gap in the wing. One has to keep in mind, however, that the feathers of the wing differ in length and therefore the

size of the gap indicated by a given raggedness score depends on the position of the gap. This was accounted for by comparing the same feathers between groups.

Ten of the moulting Dunlins were kept for a period of 17 hours to two days in cages on the seaweed, which allowed them to feed on their natural prey. The length of each growing primary was measured to the nearest 0.1 mm about every six hour.

Two adult age categories were analyzed: birds hatched the year before trapping will be referred to as 2y birds and birds hatched at least two years before will be referred to as 3y+ birds. 2y birds were identified by their still remaining juvenile inner median coverts (Prater et al. 1977), carefully considering the potential mix up with adult buff coverts (Clark 1984, Gromadzka 1985, 1986).

Results

Among the adult Dunlins trapped at Ottenby and Falsterbo during autumn migration, the proportion of birds that had initiated their wing feather moult varied between 27% and 61% in different years ($\chi^2 = 301$, d.f. = 3, $p < 0.001$, Ottenby only; Table 1). Although this applied to both 2y and 3y+ birds, the difference was most pronounced in the latter category ($\chi^2 = 141$, d.f. = 3, $p < 0.001$; $\chi^2 = 481$, d.f. = 3, $p < 0.001$, respectively). A comparison between Ottenby and Falsterbo (1988) shows no difference in the proportions of moulting birds ($p = 0.431$, Fisher's exact test). The incidence of initiated moult was higher in 2y birds than in 3y+ birds ($p < 0.001$, Fisher's exact test). The ranges over years were from 55% to 89% in 2y birds and from 8% to 55% in 3y+ birds. The adult Dunlins normally pass the southern Baltic within a rather narrow period of time

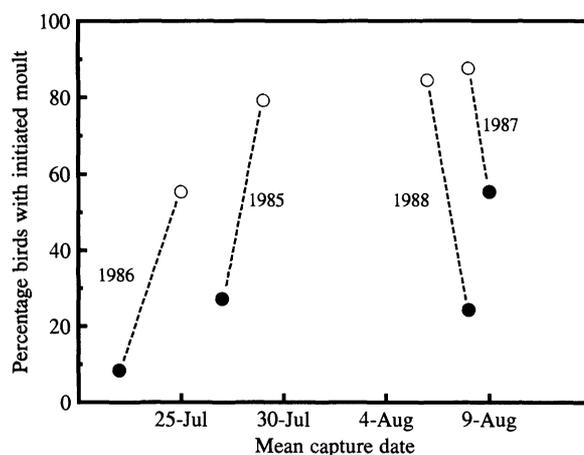
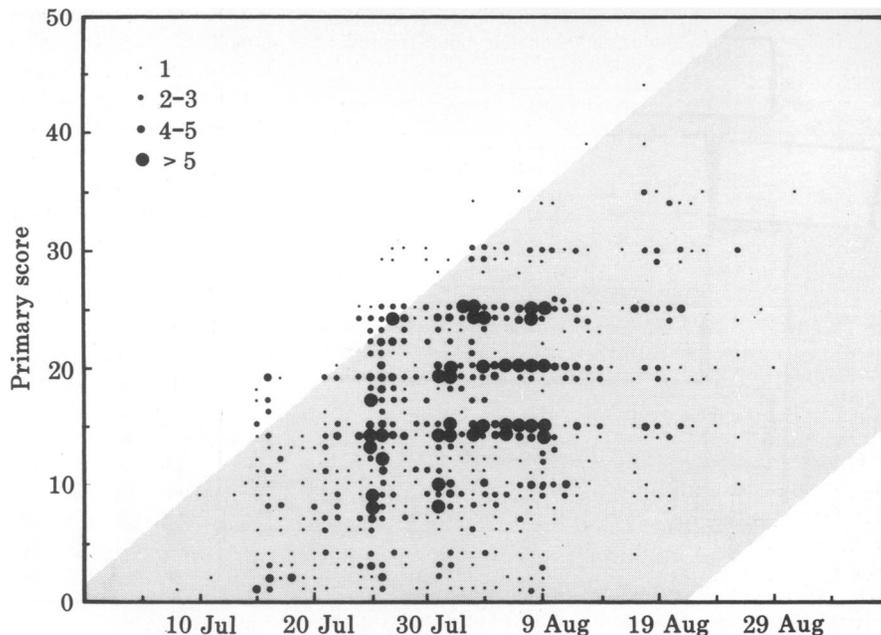


Fig. 1. Proportion of trapped Dunlins that were in moult at Ottenby, S.E. Sweden in different years plotted against mean capture date. Open circles represent 2y birds and closed circles 3y+ birds.

Fig. 2. Primary moult score of 2y Dunlins caught at different dates at Ottenby (pooled data from 1985–1988). Dots of different sizes indicate number of individuals. The shaded area, shown for comparison, comprises about 95% of the Dunlins moulting in England (Ginn and Melville 1983).



each year. In the years investigated, 45% to 72% of the birds were trapped within a period of five days. Regression of date on primary score is useful to estimate moult duration of individuals and the average date of onset in the population (Ginn and Melville 1983). However, single years cannot be used in our case. Pooling of data from different years would be permissible if the onset of moult occurs independently of the timing of migration but not if the initiation of moult and timing of migration

are correlated. Fig. 1 suggests that the former is the most likely, i.e. when the passage of adult Dunlins occurs relatively late in the season, a greater fraction is found to be moulting. We therefore pooled the Ottenby data from different years and used the variation in timing between years to get a more complete picture of the progress of moult in 2y (Fig. 2) and 3y+ birds (Fig. 3), respectively. The pictures obtained agreed with the general progress of moult in Dunlins on moulting grounds

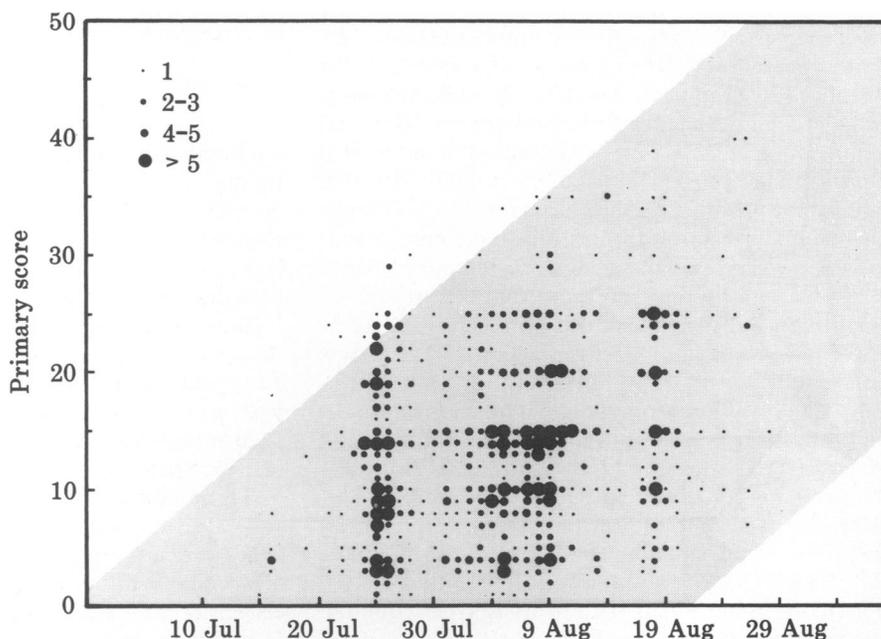


Fig. 3. Primary moult score of 3y+ Dunlins caught at different dates at Ottenby (pooled data from 1985–1988). For details, see Fig. 2.

Table 2. Mean capture date, mean primary score and mean raggedness score of Dunlins with initiated moult trapped at Ottenby in four different years.

TYear		1985	1986	1987	1988
Capture date	2y	29 jul	29 jul	9 Aug	7 Aug
	3y+	28 jul	1 Aug	9 Aug	10 Aug
Primary score	2y	16.4 ¹	12.5 ¹	16.2 ²	18.4 ²
	3y+	12.8	12.5	12.9 ³	15.8 ³
Raggedness	2y	2.0 ^{4,5}	2.1 ⁶	0.7 ⁴	0.8 ^{5,6}
	3y+	1.9 ⁷	1.8	0.8	0.9 ⁷

Significant differences between years in two-way ANOVA categorized by date and pairwise years: (1) $F_{1,292} = 31.33$, $p < 0.001$, (2) $F_{1,266} = 12.04$, $p = 0.001$, (3) $F_{1,410} = 9.68$, $p = 0.002$, (4) $F_{1,26} = 12.56$, $p = 0.002$, (5) $F_{1,191} = 26.61$, $p < 0.001$, (6) $F_{1,186} = 7.12$, $p = 0.008$, (7) $F_{1,22} = 4.89$, $p = 0.038$.

in England (shaded area in Figs 2 and 3). However, among the Ottenby birds, 2y birds were in a more advanced state than 3y+ birds ($F_{1,2244} = 110$, $p < 0.001$, ANCOVA, date on primary score).

Even if capture date had a major influence on the moult status of the Dunlins, some differences between years remained when date was accounted for in a two-way ANOVA. Only dates when at least five individuals were captured in each of the years were used. Years could only be compared pairwise, and not even all pairs of years could be compared. Capture dates of moulting birds were about ten days later in 1987 and 1988 compared with 1985 and 1986. Primary scores had a tendency to be higher in late years but when controlling for capture date, differences were only found between 1985 and 1986 and between 1987 and 1988. The pattern seemed more evident in raggedness scores: in late years birds were generally found with smaller gaps in the wing. This difference remained when the between-year effect was tested unrelated to capture date (Table 2).

As a general rule, the raggedness score was below 7 at Ottenby (Fig. 4) and Falsterbo (Fig. 5). Relatively large gaps were more common at the beginning of the moult period, whereas birds in more advanced moult tended to have smaller gaps ($F_{6,2249} = 20.9$, $p < 0.001$, ANOVA grouped by number of shed primaries 1-7; Ottenby birds only). Two (rarely three) of the innermost primaries were growing simultaneously; thereafter primaries were shed one by one and grown until nearly of full length before the next one was shed. On average 2y birds showed a higher raggedness score (1.1) than 3y+ birds (0.4; $F_{1,5504} = 438$, $p < 0.001$, ANOVA). Contrastingly, at the Wash (a major moulting site in E. England), a raggedness score below 7 generally occurs when six primaries have been shed (Johnson and Minton 1980). Moreover, the moult is typically initiated with the simultaneous shedding of the five innermost primaries. Only 6.9% of the moulting Dunlins trapped at Ottenby (Fig. 4) and 8.7% of those trapped at Falsterbo (Fig. 5), showed the same moult pattern as is typical for the Dunlins at the Wash. Even between the sites in south-

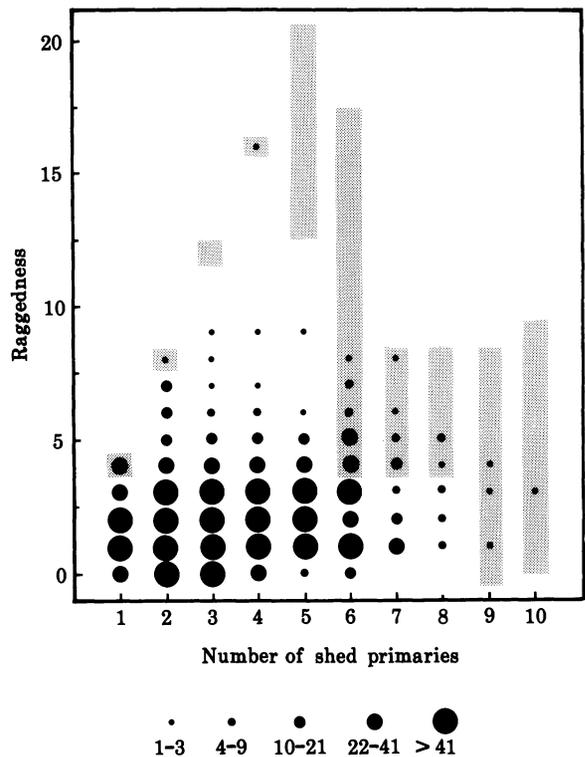


Fig. 4. Comparison of the moult schedule of Dunlins trapped during autumn migration at Ottenby 1985-1988 (filled circles) and Dunlins staging at the Wash, E. England (shaded bars). Raggedness score (the sum of lacking scores for growing feathers, Haukioja 1971) plotted against number of primaries shed. The size of the circles indicates the number of individuals. Shaded bars represent the typical moult pattern, without showing individual variation. The shedding of a primary changes the representation of an individual four steps (scores) upwards and one step (primary shed) to the right. When feathers are growing, each gain of a new primary score moves the individual one step (raggedness score) downwards in the figure.

ern Sweden, a difference in moult pattern was detected. By splitting data from 1988 into two parts at the median, the Falsterbo birds were found to be in a more advanced stage of moult ($p = 0.011$, Fisher's exact) and with higher raggedness values ($p < 0.001$, Fisher's exact) than the Ottenby birds.

Body mass was associated with raggedness values ($F_{7,5452} = 2.08$, $p = 0.042$, Two-way-ANOVA, grouped by raggedness 0-7 and age) but not with age ($F_{1,5452} = 0.09$, $p = 0.768$). Low average body masses were related to high raggedness values ($r_s = -0.883$, d.f. = 8, $p < 0.01$, Spearman rank, see Fig. 6).

Ten moulting birds were held in captivity for up to two days, in order to investigate whether feathers actually were growing. During this time, it was possible to detect and measure primary growth in all birds. Feathers in an early stage were found to grow faster than feathers in later stages, both in mm per day ($F_{2,11} = 22.5$,

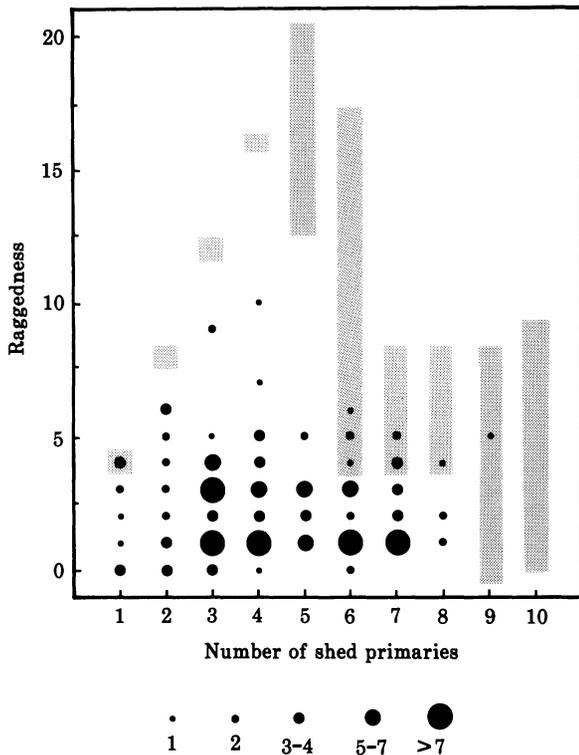


Fig. 5. Comparison of the moult schedule of Dunlins trapped during autumn migration at Falsterbo 1988 (filled circles) and Dunlins staging at the Wash, E. England (shaded bars). For details, see Fig. 4.

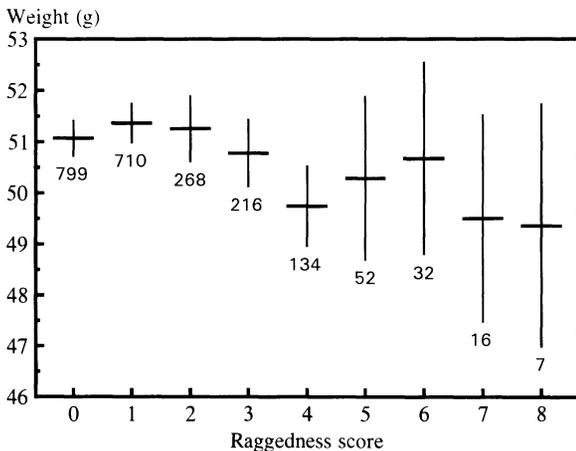


Fig. 6. Mean body mass of moulting adult Dunlins trapped at Ottenby in 1985–88 in relation to raggedness score. Horizontal lines represent the mean body mass. Vertical lines represent the 95% confidence interval of the estimate. The sample size is given below each representation. Mean body mass decreases with increasing raggedness score ($r_s = 0.883$, $p < 0.01$, Spearman rank correlation).

Table 3. Growth rate (mm d^{-1} and $\%$ of full length d^{-1}) of single primaries in different stages of growth (primary score according to Ginn and Melville 1983). Growth stage never changed between the first and the last measuring of single feathers.

Growth stage	Growth rate		Relative growth		N
	Mean	S.D.	Mean	S.D.	
Primary score 2	3.3	0.6	7.2	1.3	4
Primary score 3	1.4	0.4	2.9	0.6	2
Primary score 4	0.8	0.7	1.6	1.3	8

$p < 0.001$, ANOVA) and in percent of full length of the feather ($F_{2,11} = 28.0$, $p < 0.001$, ANOVA; Table 3).

Discussion

The Dunlins migrating through the Baltic seem to have adopted a moult pattern where the gap in the wing is smaller compared with that of Dunlins resident on the traditional moulting grounds (i.e. the Wash; Johnson and Minton 1980). One can assume that a small wing area entails a large energetical cost of flight at least at low flight speeds. It can therefore be expected that birds adjust their moult to maintain the wing area as large as possible when moult is performed during a period when they are highly dependent on flight ability (e.g. migration). The fact that larger gaps were related to leaner body masses (Fig. 6) could be an effect of increased energy costs of flight. There are, however, other possibilities. Large fat loads may be avoided to keep the energy costs below critical limits. Moreover, the ultimate cause may not be minimized energy consumption but instead to prevent decreased manoeuvrability (i.e. minimizing predation risk, e.g. Lima 1986) or minimized time on migration (Alerstam and Lindström 1990). The low proportion of birds with large gaps (Figs 4 and 5) suggests that large gaps are related to some cost that generally is avoided.

Dunlins on the coast of Morocco do not, in contrast to the birds in our study, avoid large gaps while migrating. Commonly they grow four to seven primaries simultaneously, like Dunlins resident on moulting grounds (Pienkowski and Dick 1975). The Morocco Dunlins seem to migrate in very short flights which may be related to low fat reserves according to the discussion above. Thus it seems that speed of migration and speed of moult (a large gap is at least partly due to a high speed of moult) are balancing out in the context where both cannot be maximized simultaneously. One can speculate that a fast moult is relatively more important to the Morocco Dunlins, whereas for the Baltic Dunlins it is more important to maintain a high speed of migration.

The reason why 2y birds are more advanced in the

moult schedule compared with 3y+ birds is normally assumed to be the relatively low incidence of breeding among 2y birds (c.33% in Finland, Soikkeli 1967). Thus, while 3y+ are still occupied by breeding, non-breeding 2y birds can initiate their moult (see, e.g., Gromadzka 1986 for discussion). However, the flight feathers are more worn in the 2y birds at the end of the breeding period which might "trigger" an earlier initiation of moult. The possible advantages associated with an early start of moult can be either that it enables the bird to moult at a slower rate and still finish it at the same time as otherwise, or to enjoy the benefits of a fresh plumage earlier. Johnson and Minton (1980) found that Dunlins initiating moult relatively early, moulted at a slower rate such that moult was completed more or less simultaneously with the others'. Even if the birds have reached the moulting grounds, predation risk can still be reduced by moulting at a slower rate (see above).

Studies from the moulting areas suggest that only a few Dunlins (2%, Ginn and Melville 1983, Cramp and Simmons 1983) initiate their moult prior to arrival, in contrast to our findings in the Baltic. Why this difference? The studies on the moulting grounds may not involve the same birds as those in the Baltic. However, Dunlins ringed during migration in the Baltic have rendered numerous recoveries from moulting grounds (Pettersson et al. 1986, Clark 1989, Gromadzka 1989). This is also true at Falsterbo (Roos 1984), which is situated only 250 km from the moulting grounds in Denmark. It is also unlikely that the stopover sample is considerably biased. Although 2y birds are overrepresented at Ottenby, moulting birds are not more likely to be caught than non-moulting birds (Holmgren et al. unpubl.). If birds that moult during migration shed some primaries immediately after arrival at the moulting sites (i.e. switch to the normal moult schedule), they would only be distinguishable until the fifth primary is full-grown. At present, we are unable to determine the relative contributions of "moult switching" and involvement of different populations to the observed discrepancy in moult schedule between Dunlins on migration and at moulting sites.

"A bird's energy is budgeted – that for moulting being fitted into rather short periods or, in other cases, distributed over a considerable time" (Palmer 1972, p.71). Many bird species become flightless during their wing moult (e.g. Anatidae, Alcidae, Phalacrocoracidae and most migratory Passeriformes) but in others (Accipitriiformes, Falconiformes, Procellariidae and Hydrobatidae), birds generally moult with few primaries growing concurrently during a longer period (Ginn and Melville 1983). The latter group of species are probably to such an extent dependent on their flight ability that this has priority over a rapid moult. One can assume that if a good flight ability is crucial during a restricted period, e.g. during migration, moult may be slowed down or halted during migration and speeded up afterwards

(Kjellén 1992). There are reports of other waders moulting during migration: Redshank *Tringa totanus* (Pienkowski et al. 1976), Green Sandpiper *Tringa ochropus* (Cramp and Simmons 1983) and Lapwing *Vanellus vanellus* (Snow and Snow 1976). We have ourselves observed Ringed Plover *Charadrius hiaticula*, Lapwing, Ruff *Philomachus pugnax*, Greenshank *Tringa nebularia* and Black-headed Gull *Larus ridibundus* migrating while moulting, however much less often than in the Dunlin.

Acknowledgements – Many thanks to Paul-Eric Jönsson for all help and advice. Thomas Alerstam, Nigel Clark, Meinte Engelman and Torbjörn Fagerström commented on the manuscript. Catharina Carlsén assisted in the field at Falsterbo. Staff at the bird observatories of Ottenby and Falsterbo trapped and processed the birds and computerized the data. Steffi Douwes drew the figures. Financial support for the studies at Falsterbo was received from the Danielsson Foundation (Swedish Ornithological Society). Research on bird migration at Ottenby Bird Observatory is supported by grants from the National Swedish Environment Protection Board (SNV/PMK). This is report no. 132 from Ottenby Bird Observatory and report no. 151 from Falsterbo Bird Observatory.

References

- Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. – In: Gwinner, E. (ed). Bird migration: Physiology and Ecophysiology. Springer, Berlin, Heidelberg, pp. 331–351.
- Ashmole, N. P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part I. General biology. – Ibis 103b: 235–273.
- Blomqvist, S., Frank, A. and Pettersson, L. R. 1987. Metals in liver and kidney tissues of autumn-migrating Dunlin *Calidris alpina* and Curlew sandpiper *Calidris ferruginea* staging at the Baltic Sea. – Mar. Ecol. Prog. Ser. 35: 1–13.
- Boere, G. C. 1977. The significance of the Dutch Waddensee in the annual life cycle of the arctic, subarctic and boreal waders. Part I. The function as a moulting area. – Ardea 64: 210–291.
- and Smit, C. J. 1981. Ecological data on bird species of the Wadden Sea. Dunlin. – In: Smit, C. J. and Wolff, W. J. (eds). Birds of the Wadden Sea. Final report of the section 'birds' of the Wadden Sea working group. Report Wadden Sea Wkg Grp No. 6, pp. 157–169.
- Clark, N. 1984. Ageing criteria for Dunlins. – Wader Study Group Bull. 42: 39.
- 1989. Wader migration and distribution in south west estuaries. – Contractor report, Department of Energy, U.K.
- Cramp, S. and Simmons, K. E. L. 1983. The birds of the western Palearctic, Vol. III. – Oxford University Press, Oxford.
- Farner, D. S. 1964. The photoperiodic control of reproductive cycles in birds. – Amer. Sci. 52: 137–156.
- Ginn, H. B. and Melville, D. S. 1983. Moult in birds. – BTO Guide 19, Tring.
- Greenwood, J. G. 1983. Post-nuptial primary moult in Dunlin *Calidris alpina*. – Ibis 125: 223–228.
- Goede, A. A. and Nieboer, E. 1983. Weight variation in Dunlin (*Calidris alpina*) during postnuptial moult, after application of weight data transformations. – Bird Study 30: 157–163.
- , Nieboer, E. and Zegers, P. M. 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.
- 1986. Primary moult of adult Dunlins *Calidris alpina* of different age during autumn migration. – *Vår Fågelvärld Suppl.* 11: 51–56.
- 1989. Breeding and wintering areas of Dunlin migrating through southern Baltic. – *Ornis Scand* 20: 132–144.
- Hale, W.G. 1980. *Waders*. – Collins, London.
- Haukioja, E. 1971. Processing moult card data with reference to the chaffinch *Fringilla coelebs*. – *Ornis Fennica* 48: 25–32.
- Johnson, C. and Minton, C. D. T. 1980. The primary moult of the Dunlin *Calidris alpina* at the Wash. – *Ornis Scand.* 11: 190–195.
- Kendeigh, S. C. 1949. Effect of temperature and season on the energy resources of the English sparrow. – *Auk* 66: 113–127.
- Kjellén, N. 1992. Differential timing of autumn migration between sexes and age groups in raptors at Falsterbo, Sweden. – *Ornis Scand.* 23: 420–434.
- Lilja, I. 1969. On the postnuptial wing moult of migratory Dunlin *Calidris alpina*. – *Porin Lintutieteellinen Yhdistys Vuosikirja* 1968: 40–43.
- Liljefors, M., Pettersson, J. and Bengtsson, T. 1985. Recruitment areas for migrants trapped at Ottenby Bird Observatory. – Special report from Ottenby Bird Observatory No. 5, Ottenby Fågelstation, Degerhamn.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. – *Ecology* 67: 377–385.
- Palmer, R. S. 1972. Patterns of moulting. – In: Farner, D. S., King, J. R. and Parkes, K. C. (eds). *Avian biology*. Vol. II. Academic Press, New York, pp. 65–102.
- Payne, R. B. 1972. Mechanisms and control of molt. – In: Farner, D. S., King, J. R. and Parkes, K. C. (eds). *Avian Biology*. Vol. II. Academic Press, New York, pp. 103–155.
- Pettersson, J., Sandström, A. and Johansson, K. 1986. Wintering areas of migrants trapped at Ottenby Bird Observatory. – Special report from Ottenby Bird Observatory No. 6, Ottenby Fågelstation, Degerhamn.
- Pienkowski, M. W. and Dick, W. J. A. 1975. The migration and wintering of Dunlin *Calidris alpina* in north-west Africa. – *Ornis Scand.* 6: 151–167.
- , Knight, P. J., Stanyard, D. J. and Argyle, F. B. 1976. The primary moult of waders on the Atlantic coast of Morocco. – *Ibis* 118: 347–365.
- and Pienkowski, A. E. 1983. WSG project on the movements of wader populations in western Europe: eighth progress report. – *Wader Study Group Bull.* 38: 13–22.
- Prater, A. J., Marchant, J. H. and Vuorinen, J. 1977. Guide to the identification and ageing of Holarctic waders. – *BTO Guide* 17, Tring.
- Roos, G. 1984. Migration, wintering and longevity of birds ringed at Falsterbo (1947–1980). – *Anser*, Suppl. 13. (In Swedish with English summary.)
- Snow, D. and Snow, B. 1976. Post-breeding moult of the lapwing. – *Bird Study* 23: 117–120.
- Soikkeli, M. 1967. Breeding cycle and population dynamics in the Dunlin *Calidris alpina*. – *Ann. Zool. Fennici* 4: 158–198.
- 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.
- Stresemann, E. 1967. Inheritance and adaptation in molt. – *Proc. XIV Int. Orn. Congr.*: 75–80.
- Svensson, L. 1984. Identification guide to European passerines. Third ed. – Lars Svensson, Stockholm.

(Received 20 February 1991, revised 31 March 1992, accepted 15 July 1992.)