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

Noël Holmgren, Hans Ellegren and Jan Pettersson

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 mouling 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.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>3y+</th>
<th>2y</th>
<th>Total</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ottenby</td>
<td>1985</td>
<td>25.8</td>
<td>27.2</td>
<td>40.6</td>
<td>1562</td>
</tr>
<tr>
<td>Ottenby</td>
<td>1986</td>
<td>39.3</td>
<td>8.4</td>
<td>26.9</td>
<td>1443</td>
</tr>
<tr>
<td>Ottenby</td>
<td>1987</td>
<td>18.8</td>
<td>25.4</td>
<td>46.2</td>
<td>1032</td>
</tr>
<tr>
<td>Ottenby</td>
<td>1988</td>
<td>30.9</td>
<td>24.3</td>
<td>55.2</td>
<td>1186</td>
</tr>
<tr>
<td>Falsterbo</td>
<td>1988</td>
<td>27.3</td>
<td>26.6</td>
<td>43.9</td>
<td>362</td>
</tr>
</tbody>
</table>

In 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 (2y: $\chi^2 = 141$, d.f. = 3, $p < 0.001$; 3y+: $\chi^2 = 481$, 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.
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 moultng. 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 moultng grounds.
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 (F1,224 = 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 (F1,224 = 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; F1,55u = 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 southern 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 (F7,545 = 2.08, p = 0.042, Two-way-ANOVA, grouped by raggedness 0-7 and age) but not with age (F1,545 = 0.09, p = 0.768). Low average body masses were related to high raggedness values (r = -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. Featherg in an early stage were found to grow faster than feathers in later stages, both in mm per day (F2,11 = 22.5,

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

<table>
<thead>
<tr>
<th>Year</th>
<th>1985</th>
<th>1986</th>
<th>1987</th>
<th>1988</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capture date</td>
<td>2y</td>
<td>29 Jul</td>
<td>29 Jul</td>
<td>9 Aug</td>
</tr>
<tr>
<td>Primary score</td>
<td>3y+</td>
<td>28 Jul</td>
<td>1 Aug</td>
<td>9 Aug</td>
</tr>
<tr>
<td>Raggedness</td>
<td>2y</td>
<td>16.4</td>
<td>12.5</td>
<td>16.2</td>
</tr>
<tr>
<td></td>
<td>3y+</td>
<td>12.8</td>
<td>12.5</td>
<td>12.9</td>
</tr>
</tbody>
</table>

Significant differences between years in two-way ANOVA categorized by date and pairwise years: (1) F1,224 = 31.33, p < 0.001, (2) F1,226 = 12.04, p = 0.001, (3) F1,430 = 9.68, p = 0.002, (4) F1,236 = 12.56, p = 0.002, (5) F1,198 = 26.61, p < 0.001, (6) F1,184 = 7.12, p = 0.008, (7) F1,22 = 4.89, p = 0.038.
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.

<table>
<thead>
<tr>
<th>Growth stage</th>
<th>Growth rate</th>
<th>Relative growth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>S.D.</td>
</tr>
<tr>
<td>Primary score 2</td>
<td>3.3</td>
<td>0.6</td>
</tr>
<tr>
<td>Primary score 3</td>
<td>1.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Primary score 4</td>
<td>0.8</td>
<td>0.7</td>
</tr>
</tbody>
</table>

$p < 0.001$, 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
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.

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