# Incomplete and irregular annual replacement of secondaries in Eurasian Golden Plovers, *Pluvialis apricaria*

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In most waders (Charadrii) replacement of old by new feathers during moult of primaries occurs in a fixed order and in such a way that flight capacities are maintained. Moult of the secondaries of the Eurasian Golden Plover *Pluvialis apricaria* deviates from this general pattern. The sequence of secondary moult is irregular and – in most cases – asymmetric between wings. In addition, only about half the secondaries are renewed every year. Secondary moult is arrested in October and not resumed in spring. This can be deduced from the moult scores of >900 adults that were caught in autumn and spring when staging in the Netherlands, and from inspection of three birds caught on their nests in Iceland. It is also confirmed by the moult scores of seven birds (from a group of about 1,500) that were recaptured after their first complete moult. As their juvenile secondaries had been marked with picric acid the year before, all non-dyed secondaries had evidently been renewed – and all dyed ones were old. As irregular moult of the secondaries also occurs in other Charadriidae plovers, this characteristic might have originated from a common ancestor. Irregular and incomplete secondary moult may be explained by birds avoiding the costly moult of feathers that experience little wear. With most moult studies focusing on primary moult, this aspect of secondary moult has previously remained undiscovered.

## INTRODUCTION

Moult may be considered as the rather precisely timed replacement of individual feathers. The process is tightly interwoven with each bird's life-history including reproduction, migration and its adaptations for recruitment and survival (e.g. Jacobs & Wingfield 2000, Noordhuis 1989, Palmer 1972, Stresemann & Stresemann 1966). Waders tend to replace their large wing and tail feathers once a year (Cramp & Simmons 1983, Ginn & Melville 1993, Glutz von Blotzheim *et al.* 1975, Marchant & Higgins 1993, Paulson 1993, Piersma *et al.* 1996, Rogers 1996), but in most species the contour feathers of the body are moulted more often. The changes in external appearance associated with such moults may be clues for temporarily varying selection pressures that are acting on the birds (Jukema & Piersma 1987, 2000, Piersma & Jukema 1993, Piersma *et al.* 2001).

In some species, the moult of one or more feather tracts may stop before it is completed. This is most conspicuous in the large flight and tail feathers. It may occur when the bird needs to invest heavily in other processes or activities, such as migration and breeding (e.g. Buehler & Piersma 2008, Summers *et al.* 2004). Subsequent to this, moult may be resumed or further delayed to the next moulting cycle. Delay within the same moulting cycle is generally described as suspended moult, delay until the next moulting cycle as arrested moult (e.g. Prater *et al.* 1977, Waldenström & Ottosson 2002).

In Eurasian Golden Plovers *Pluvialis apricaria* (Charadrii) the primaries are replaced in the descendant fashion typical of all waders (Henriksen 1985, Jukema 1982, Koopman 2012). However, the replacement of the secondaries is odd. Not every secondary appears to be moulted every year (Jukema *et al.* 2001). Secondary moult stops during the winter (Jukema 1982, Jukema *et al.* 2001), but until now it has not been clear whether it is resumed in spring. In addition, the order in which the 11 secondaries are replaced is irregular. In this study we aim to document and to discuss the diverse moult patterns in the secondaries of Eurasian Golden Plovers.

**Fig. 1.** Upper side of the right wing of a second calendar year Eurasian Golden Plover in October after its first moult cycle. The large feathers on the left are primaries. Secondary moult formula is 40000005525, but the tenth secondary (score '2') is not visible. The six secondaries that are unmoulted (score '0') differ in colour and wear (they are browner and have especially worn tips) from the three that have recently been replaced (score '5') on the right (greyer and with sharp edges).

**Fig. 2.** The tip of the underside of the secondaries of a Eurasian Golden Plover are dyed with picric acid in a 2-cm wide yellow strip in April 1992 at Workum, Friesland, N Netherlands.

## METHODS

Eurasian Golden Plovers were trapped in the north of the Netherlands using 'wilsternets', which are large traditional 3.5 × 25 m largely wind-powered nets. They are specifically designed to capture single or small flocks of Eurasian Golden Plovers in midair after they have been attracted to the netting area using whistles and live and dead decoys (Jukema *et al.* 2001). Captured birds were staging in the Netherlands and associated with breeding areas in Scandinavia and NW Russia (Byrkjedal &Thompson 1998, Jukema *et al.* 2001).

Upon capture birds were ringed and measured, and their moult scores noted. In this study only the stage of moult of the 11 individual secondaries of each wing will be considered. The data were collected in Friesland, N Netherlands, by J. Jukema in 1980–1981 and 1987–1989 on adult birds (≥1 year old) and in 1991–1994 (1 year old, recaptured after treatment during the previous year – see below) and in North Holland, W Netherlands, by T. Pieters in 1977–1998 on adult birds (≥1 year old). Each feather (numbered 1–11 from outermost to innermost) was scored on a 5-point scale where '0' represents an unmoulted old feather, '1' a missing old feather or a new feather in pin, '2' a new feather just emerging from the sheath up to a third grown, '3' a half grown feather, '4' a new feather more than two-thirds grown with a waxy sheath at its base and '5' a fully developed new feather (Ginn & Melville 1983). Old secondaries that were not moulted (score '0') can easily be distinguished in the field from the new secondaries (score '5') by colour differences and wear (Fig. 1).

*Moult percentage* was calculated by adding the moult scores of all the secondaries of both wings (a maximum score of 5 for 22 feathers = 110) and dividing by 1.1. *No secondary moult* was defined by the presence of only old secondaries with score 0. *Active* secondary moult was defined by the presence of one or more secondaries with scores 1, 2, 3 or 4. *Arrested* secondary moult was defined by the presence of old and new secondaries with scores 0 and 5 but none with a score of 1, 2, 3 or 4. *Completed* secondary moult was defined by the presence of only new secondaries with score 5.

To find out to what extent secondary moult is resumed after the winter, we compared the proportions of renewed secondaries in autumn (192 birds caught in November and December in 1980, 1987 and 1988 in Friesland) and spring (231 birds caught from the end of February up to the end of


**Fig. 3.** Upperside (A) and underside (B) of the left wing of a Eurasian Golden Plover (the first one in Fig. 8) after its first large-feather moult. This bird had been first caught, ringed and marked with picric acid on the tips of its secondaries when it was a juvenile on 21 Nov 1990. It was recaptured on 27 Nov 1991 when its secondary moult-score pattern was 55550005555. This can be seen easily in photo B which shows the three yellow secondaries (score '0') in the middle. The same three secondaries can also be recognized in photo A as somewhat shorter, more worn and without a light fringe.

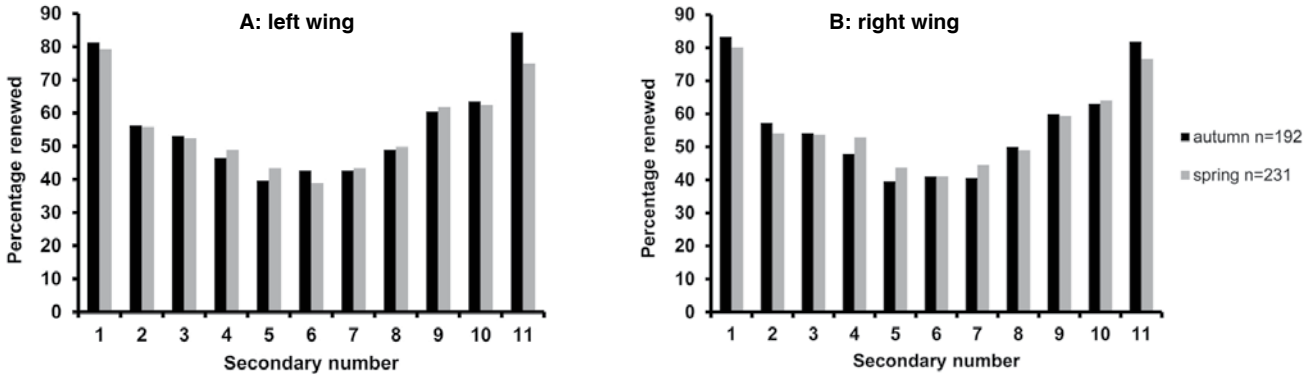


**Fig. 4.** Comparison of the percentage of replaced feathers (moult score 5) in adult (≥1 year old) Eurasian Golden Plovers for both the left and the right wing in autumn (n = 192) and spring (n = 231).

April in 1981, 1988 and 1989 in Friesland). The data for the birds with moult scores for all secondaries of both wings were analysed for each month to determine the timing of moult (572 birds from Friesland and 334 from North Holland). To find out whether secondary moult is completed on the breeding grounds, three birds were examined that had been caught on 1 and 2 June 2002 in walk-in cages at their nests in Iceland.

To determine the progress of the moult cycle within individuals, the secondaries of about 1,500 birds were marked with picric acid during September–April, 1990–1993 (Fig. 2). Among juveniles, only those that had not moulted any flight-feathers (primaries and secondaries) were marked. The tip of the underside of all their secondaries was dyed with a 2 cm yellow stripe. Upon recapture after their first moult, their secondary moult scores were very clear from the pattern of old dyed feathers and new undyed ones (Fig. 3).

## RESULTS

For each of the 11 secondaries, the percent that have been renewed (score '5') in autumn and spring is almost identical in both wings (Fig. 4) showing that moult is not resumed in early spring. About half of the secondaries are renewed during the main large-feather moult in summer and early autumn (Figs 4, 5 & 6), but more of the outermost and innermost secondaries are renewed than those in the middle (Fig. 4). The general pattern of secondary moult in the left and right wings is similar (Fig. 4). However, close inspection of the moult scores of individuals shows that the pattern of secondary moult in each wing is frequently different. Among the captured birds only 29 % in Friesland (n = 574) and 28% in North Holland (n = 334) had exactly the same pattern of moult-scores in the secondaries of both wings. Therefore an asymmetry score was determined by adding the differences between the moult scores of all corresponding secondaries in the two wings. This is minimal (0 or 0%) when the moulting pattern in both wings is identical and maximal when there are old and new secondaries *and* if all fresh full grown feathers in the one wing correspond to old feathers in the other (55 or 100%). Among the birds that were captured the average asymmetry score was 13% in Friesland and 14% in North Holland and hardly changed at all between the end of the year and the following spring (Fig. 5).

Our results show that in Eurasian Golden Plovers, secondary moult proceeds in an irregular order. It may start at different sites in the secondaries tract, and there may be more than one centre of active moult at the same time. Therefore one measure of irregularity is the number of centres of active moult. In birds that moult their secondaries in linear succession only one centre of active moult is present in each wing. Our results show that pattern is extremely rare among Eurasian Golden Plovers. The number of active moult centres

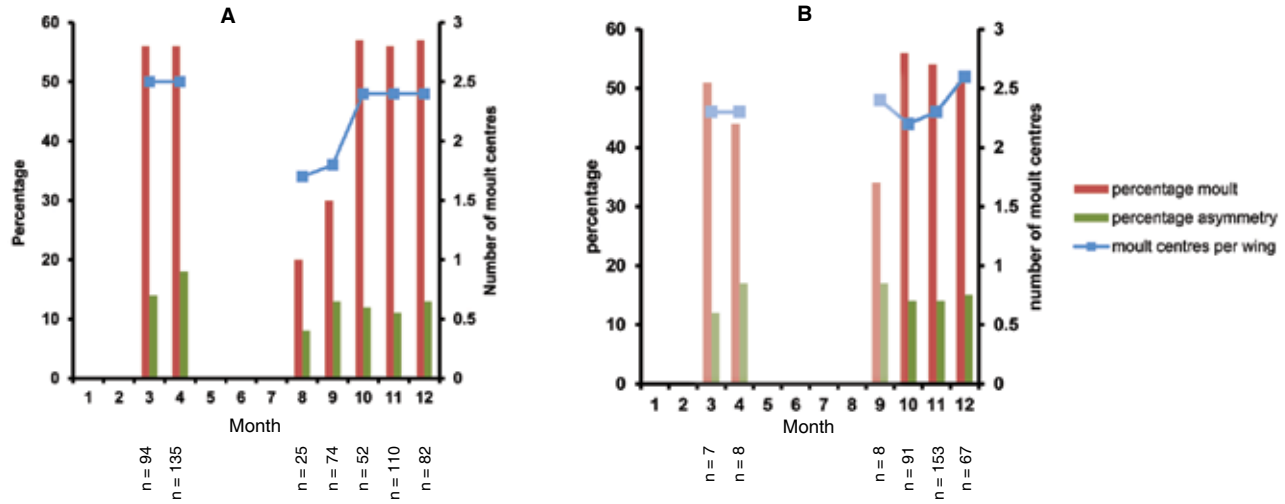


**Fig. 5.** Temporal characteristics of secondary moult in adult (≥1 year old) Eurasian Golden Plovers in Friesland (A) and North Holland (B): percentage moult, percentage asymmetry and mean number of centres of active moult (as defined in Methods) in each wing plotted against month (the data for North Holland in March, April and September are shown in pale colours because they are based on small samples).

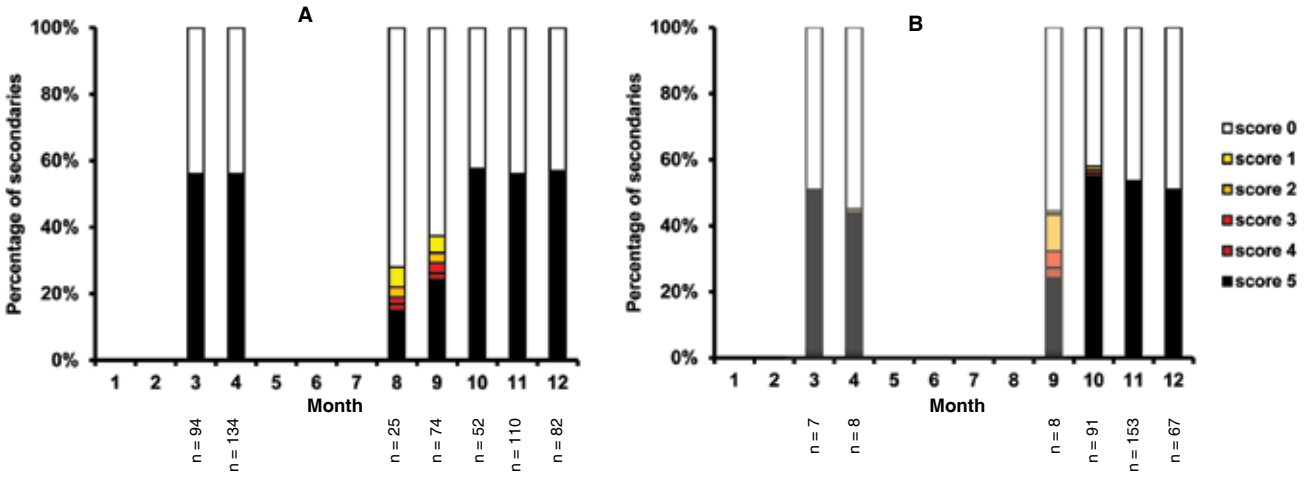


**Fig. 6.** Temporal characteristics of secondary moult in adult (≥1 year old) Eurasian Golden Plovers in Friesland (A) and North Holland (B): Percentage of secondaries with different moult scores (as defined in Methods) plotted against month (the data for North Holland in March, April and September are shown in pale colours because they are based on small samples).

in the captured birds varied between 0 (all secondaries old) and 5, but was most often between 1 and 3. On average, 2.3 moult centres per wing were counted in both Friesland and in North Holland and there was virtually no change in their number between the end of the year and the following spring (Fig. 5). Moult percentage showed an increase from August to October to about 55% and then remained steady until the end of the year and throughout the following spring (Fig. 5).

Primary moult in Eurasian Golden Plovers takes place in autumn and finishes around October (Byrkjedal &Thompson 1998, Henriksen 1985, Jukema 1982, Jukema *et al.* 2001, Koopman 2012), and it seems that at the same time the moult of the secondaries becomes arrested (Fig. 6). A comparison between Friesland and North Holland was possible only for October to December, when sufficient numbers of birds were caught in both areas (Figs 5–7). This shows that all birds are in arrested secondary moult in this period. However, the North Holland data are insufficient to draw conclusions on when the birds go into arrested moult, nor do they give much information on the period of active moult. Nevertheless the similarities between the Friesland and North Holland datasets are remarkable. Although both were collected by different observers, and maybe based on slightly different populations, the secondary moult patterns and trends they show are almost identical.

Active secondary moult occurred in August and September, but not in any of the other months when plovers were caught (Fig. 6). About 80% of birds caught in August and September were in active secondary moult, but in the other months almost all had arrested secondary moult with a mixture of old and new secondaries. Very few birds were caught that had only old or only new secondaries (Fig. 7).

Secondary moult of the previous moulting cycle had not been completed in any of the three birds that were caught on their nests in Iceland. The irregular distribution of (heavily) worn secondaries corresponded to what had been observed in the winter quarters. The three birds were almost two years old or older. They had started already a new wing moult cycle and had lost 1–2 inner primaries (primary moult scores: 3200000000, 2000000000 and 1000000000), but had no active secondary moult.

Out of about 1,500 Golden Plovers that were caught as juveniles and had their secondaries dyed yellow, seven were recaptured after their first complete moult (Fig. 8). Because

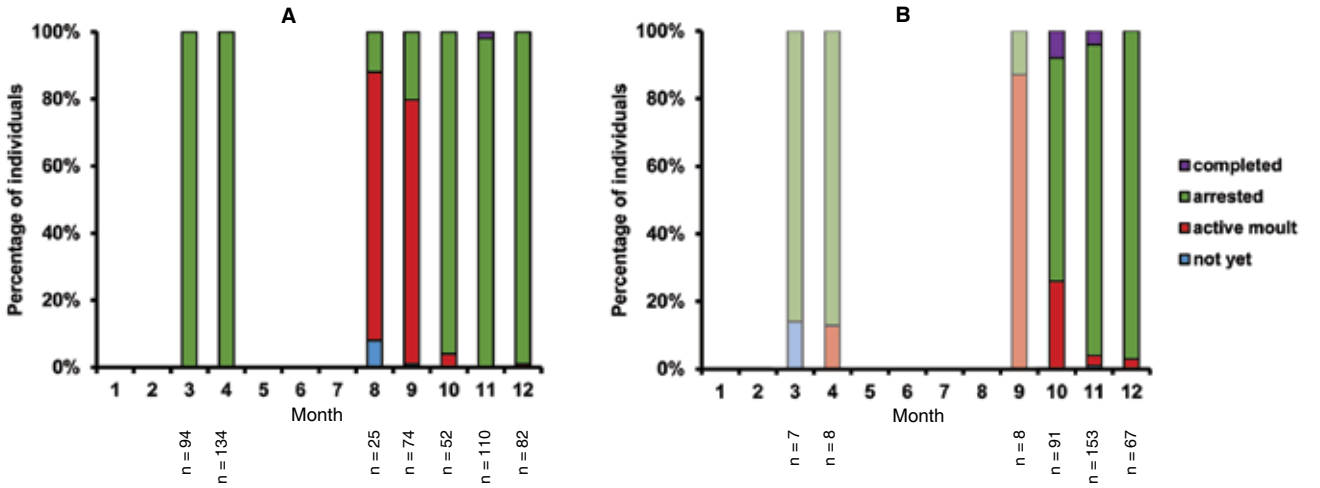


**Fig. 7.** Temporal characteristics of secondary moult in adult (≥1 year old) Eurasian Golden Plovers in Friesland (A) and North Holland (B): Percentage of birds that have not yet started secondary moult, in active secondary moult, in arrested secondary moult or having completed secondary moult plotted against month (the data for North Holland in March, April and September are shown in pale colours because they are based on small samples).

of the dyeing, the secondaries that were not renewed could easily be recognized. Only the outer and inner secondaries had been renewed after the first moulting period and thus many of the central secondaries (almost 40% of the total) were old. As the first complete moult proceeds in the summer and autumn of their second calendar year (and the second complete moult one year later), the secondaries that are not renewed have to be used for at least two years. In three birds of this sample secondary renewal in the left and right wing is not symmetric (for instance the third bird in Fig. 8). As Eurasian Golden Plovers were rarely recaptured, it could not be established how secondary moult proceeds in successive years. However, various observations in the field suggest that there is considerable variation between individuals in patterns of secondary moult. The general pattern (see Fig. 4), with a higher proportion of renewed outer and inner secondaries, may therefore be influenced strongly by 1–2 year old plovers that represented 20–30% of the catches.

## DISCUSSION

This study presents evidence that secondary moult in Eurasian Golden Plovers is normally incomplete. First, birds of which all juvenile secondaries were dyed with picric acid were seen to retain about half of dyed secondaries after their first wing moult cycle. They were shown to *exclusively* renew their outer and inner secondaries. Second, in adults the percentage of renewed secondaries, remained at just over half between autumn and the following early spring. The outer and inner secondaries tended to be renewed more often as the others, but this observation might be largely or wholly determined by the inclusion of 1–2 year old birds. Third, the breeding birds in Iceland had both very old (>1 year old) and fairly recent (<1 year old) secondaries, suggesting that secondary moult had been arrested in the autumn of the preceding year. However, this latter observation should be treated with some caution, as the sample is small and most birds from Iceland do not winter in the Netherlands. However, only the Eurasian Golden Plovers from the Icelandic population have to make a transatlantic flight and thus need good flight feathers. If they are able to do so with a set of only partially renewed secondaries, there does not seem to be a need for birds from other populations to renew all their secondaries either.

According to Glutz von Blotzheim *et al.* (1975) moult of the secondaries in Eurasian Golden Plovers starts when primary 7 is still growing. This suggests a general, regular pattern of secondary moult. However, our results show that it is not straightforward and is a rather complicated and irregular process. By treating each secondary separately, we have been able to give a fairly complete description of secondary moult in Eurasian Golden Plovers which shows that it is clearly distinct from primary moult. The two processes differ in pattern and timing. Moreover, secondary moult in Eurasian Golden Plovers is distinct from secondary moult in most other small–medium size birds for which information is available. The order is irregular and, quite often, moult is asymmetric between the two wings. Secondary moult in other birds tends to be regular. It is usually ascendant, starting with the outermost secondary and progressing inwards towards the body. Yet, there are various bird groups with alternative patterns of secondary moult (Ginn & Melville 1983, Noordhuis 1989, Stresemann & Stresemann 1966). Most waders have this ascendant moult pattern, and in most waders moult of the secondaries starts when moult of the primaries is halfway with a moult score of 20–30 (Boere 1976, Ginn & Melville 1983, Prater *et al.* 1977).

Contrary to previous statements (e.g. Glutz von Blotzheim *et al.* 1975), the Eurasian Golden Plover starts secondary moult well before moult of the primaries is half complete. Primary moult starts early, during the breeding season, as shown by the birds that were examined in June in Iceland. Such an early start was also observed in Eurasian Golden Plovers that were caught in Sweden on their nests (P. Olsson, pers. comm.). In the Peak District in England, between Sheffield and Manchester, primary moult had already started in some of the breeding Eurasian Golden Plovers that were caught in May and in all that were caught in June (Yalden & Pearce-Higgins 2002). Secondary moult probably starts shortly after breeding, as it has already begun in the first birds to arrive in the Netherlands in August (Fig. 6). Many fully-grown new secondaries (moult score '5') are present at that time. The moult-score of the primaries is then only 30–35 (Byrkjedal & Thompson 1998, Henriksen 1985, Jukema 1982, Jukema *et al.* 2001, Koopman 2012). Occasionally it has been recorded that the first secondary has already been renewed when primary moult begins (Byrkjedal & Thompson 1998, p. 82, Plate 38).

Irregular and seemingly chaotic moult of the secondaries has also been found in the other three *Pluvialis* species: Pacific Golden Plover *P. fulva*, American Golden Plover *P. dominica* and Grey Plover *P. squatarola* (J. Jukema, pers. obs.; P. Olsson, pers. comm.; E. Wymenga, pers. comm.) and in other plover species such as Northern Lapwing *Vanellus vanellus* (J. Jukema, pers. obs.; Roselaar 2007), Dotterel *Charadrius morinellus* (J. Jukema, pers. obs.), Double-Banded Plover *Charadrius bicinctus* (M. Barter & C. Minton, pers. comm.) and Lesser Sand Plover *Charadrius mongolus* (P. Olsson, pers. comm.). All these species belong to the family Charadriidae. Clearly, more plover species may be found to have irregular secondary moult if only it is looked for. Moreover, highly irregular and incomplete secondary moult is found in a more distantly related species, the Eurasian Stone-curlew *Burhinus oedicnemus* (Giunchi *et al.* 2008), which also belongs to the Charadrii suborder.

All the examples found so far suggest that irregular secondary moult is a typical character of the Charadrii originating from a common ancestor (Byrkjedal & Thompson 1998, Piersma *et al.* 1996). It could have evolved because most species of the Charadrii breed in the tropics and neo-tropics. These species do not have long migrations, and hence experience little wear of feathers. Because of that they can afford to spread the energetically expensive process of moult over a longer period, for example by moulting only a proportion

**Fig. 8.** Moult-score pattern of the secondaries of seven Eurasian Golden Plovers that had the tips of their secondaries colour-dyed when they were juveniles during September–April before their first large-feather moult and recaptured during October–April after that moult.

| Left wing | Right wing |
|---|---|
| 55550005555 | 55550005555 |
| 55000055555 | 55000055555 |
| 55000000055 | 55000050555 |
| 55500005555 | 55500000555 |
| 55500000555 | 55500000555 |
| 55555005555 | 55555055555 |
| 55000005555 | 55000005555 |

of their secondaries each year. It should be stressed, however, that more data are needed on the moult of secondaries in waders, other than the four *Pluvialis* species, for a better understanding of the significance of irregular moult. In another publication we will demonstrate the close association between secondary moult and migratory behaviour in the *Pluvialis* group (Jukema *et al.* unpubl.).

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