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In tundra plovers the frequency of inner flight feather replacement varies with length of long-distance flights

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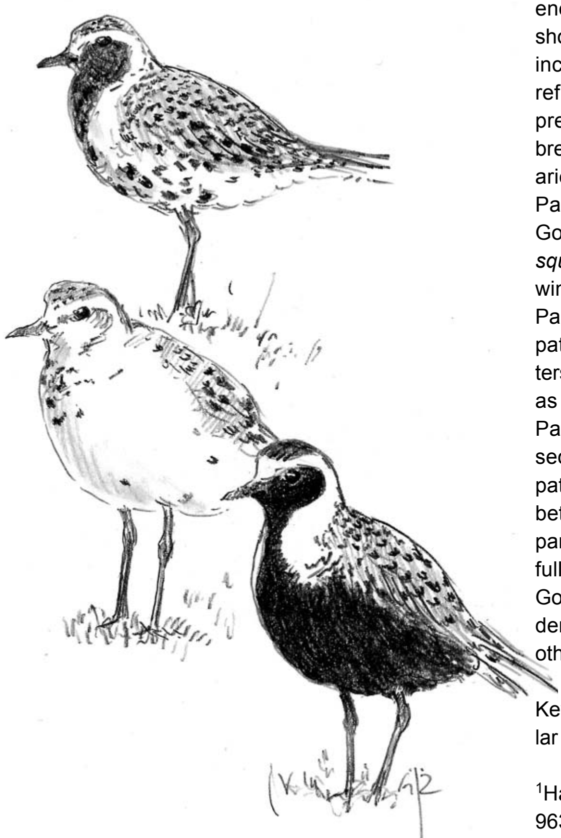

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The repair jobs that birds have to do to maintain high quality plumage take energy and time, so should be under intense selection. Recently, we have shown that secondary moult in the Eurasian Golden Plover *Pluvialis apricaria* is incomplete, irregular and asymmetric between wings, and argued that this reflected their 'relaxed' migratory habits. On the basis of this hypothesis, we predict that relatives of this species that have to make long flights between breeding areas and winter quarters would invest more in the moult of secondaries. To test this we collected data on moult patterns in two populations of Pacific Golden Plovers *Pluvialis fulva* (Siberia and Alaska), on American Golden Plovers *Pluvialis dominica* (Alaska) and Grey Plovers *Pluvialis squatarola*. Data were from the breeding, staging (Mongolia and Indiana) and wintering (Uruguay) areas. We found patterns consistent with our prediction: Pacific Golden Plovers from Siberia, and Grey Plovers have a similar moulting pattern to Eurasian Golden Plovers. Although both go to remote winter quarters, they migrate mainly over land, probably making short or moderate flights, as they are able to stage frequently. In contrast, the Alaskan populations of Pacific Golden Plovers and American Golden Plovers tend to renew all their secondaries from their second wing moult onwards. In line with their moult patterns, these two populations are known to make very long non-stop flights between breeding and winter areas. We argue that irregular moult and the partial renewal of secondaries is a primitive character in all four species. The full replacement of secondaries in the Pacific Golden Plovers and American Golden Plovers from Alaska may be considered as an adaptation for very long demanding flights. Regular moult patterns of secondaries, as found in many other shorebirds, could be a further refinement of this adaptation.

Key words: Golden Plover, *Pluvialis* spp., Grey Plover, secondary moult, irregular moult, arrested moult, migration, non-stop flight, evolution, primitive character

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The quality of the large flight feathers – primary and secondary – may be critical for migrating birds, especially for those that have to make long non-stop flights. Excessive wear is precluded by the yearly renewal of most of these feathers. Their quality may depend on moult characteristics, such as speed (e.g. Serra 2001). Completeness of moult, its timing and the locations where it proceeds, are interconnected with various life history features, such as residence duration and food availability in breeding, staging and winter areas (e.g. Holmgren & Hedenström 1995, Barta *et al.* 2008, Dietz *et al.* 2013). In particular, in Arctic-breeding birds, time schedules may be very tight, forcing them to postpone moult – partly or completely – until they have reached their winter quarters (e.g. Buehler & Piersma 2008, Conklin & Battley 2012).

As for any other character, timing and sequence of moult of the different feather tracts has been shaped by natural selection (Piersma 2004). Flight capacity is impaired by the loss of an old flight feather before the new one can appear. The loss of a primary, above all an outer primary, has effects on flight speed, whereas the loss of a secondary mainly affects lift (Jenni & Winkler 1994, Swaddle & Witter 1997, Hedenström & Sunada 1999). Feather loss should be programmed in such a way that minimises the impairment of flight capacity. Models predict that different feather types are moulted at different times, that the primaries are moulted in a descending way (inner to outer) and that the order of replacement of the secondaries is not necessarily regular (Barta *et al.* 2006).

In Eurasian Golden Plovers (EGP) *Pluvialis apricaria*, secondary moult has been shown to be irregular, asymmetric between wings and incomplete (Jukema 1982, Henriksen 1985, Jukema *et al.* 2013). We ascribed this phenomenon to relaxed migration habits. Probably, the selection pressures for thorough and systematic flight feather moult are not very strong and dominated by other selection pressures. Although many of these birds travel fairly long distances to reach their winter areas in western Europe and the Mediterranean (Figure 1A), their daily movements are not very extensive (e.g. Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983, Byrkjedal & Thompson 1998, Jukema *et al.* 2001). During the non-breeding period EGP usually stay and move about in flocks. Apart from the birds from Iceland that have to fly at least 420 km to reach the Faroe Islands or 750 km to reach the Scottish mainland, there is no need to make long non-stop flights.

Three other species belong to the tundra plovers (Byrkjedal & Thompson 1998), genus Pluvialis: Pacific Golden Plover (PGP – Figure 1B) *Pluvialis fulva*, American Golden Plover (AGP – Figure 1C) *Pluvialis dominica* and Grey Plover (GP – Figure 1D) *Pluvialis squatarola*. In all three the distances between breeding and wintering areas are considerably larger than in EGP. In addition, in AGP and in PGP from Alaska very long non-stop flights have to be made. It is plausible that selection pressures for thorough and systematic flight feather moult are stronger in these species than in EGP. One may therefore predict that PGP, AGP and GP show more complete and more regu-

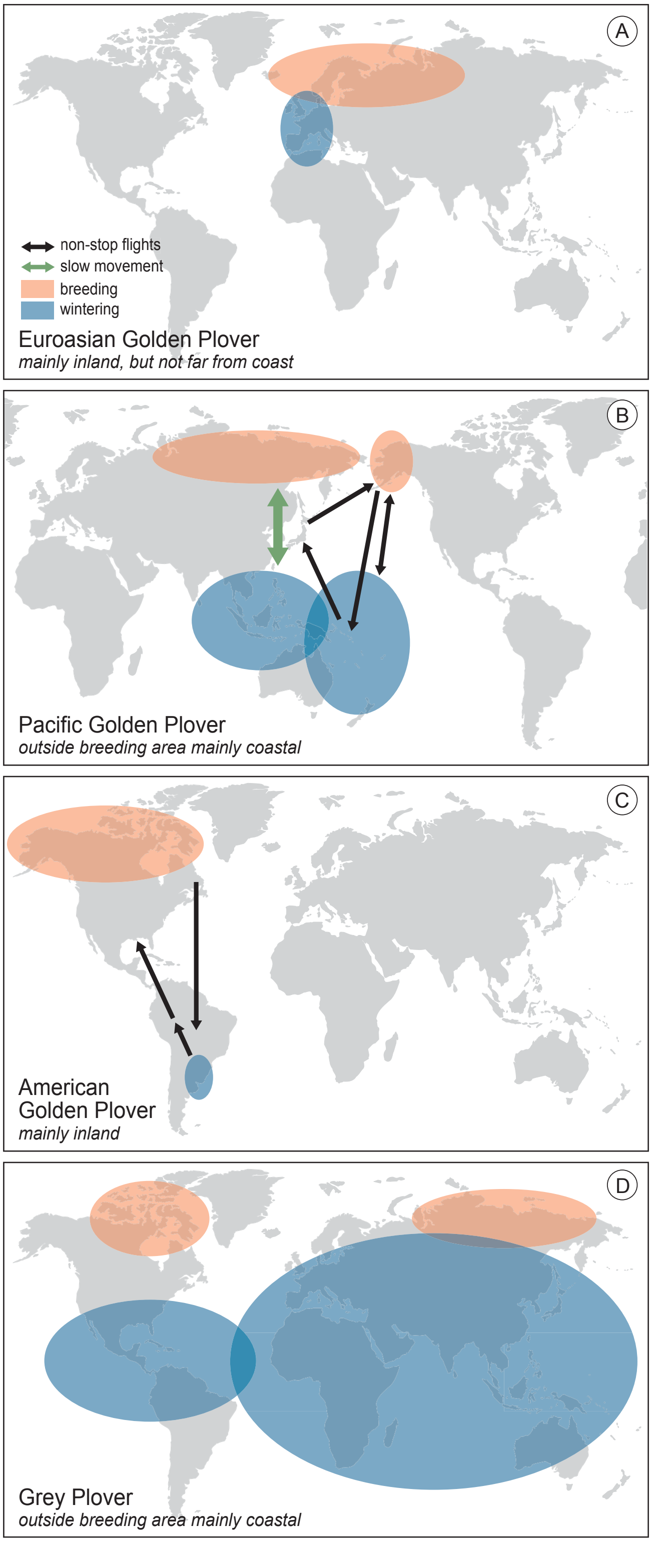

Figure 1. Schematic breeding and wintering distribution of the four species of tundra plovers (after: Byrkjedal & Thompson 1998, Johnson & Connors 2010).

lar replacement of secondary feathers than EGP. In the present study we test this prediction by an examination of moult patterns on the basis of original field work. We also compared the migration strategies of the four *Pluvialis* species in detail, mainly by examining the literature. We tried to consider these strategies as broadly as possible, taking total migration distance, non-stop flights, capacities to store fat, wing quality and age at first breeding into consideration.

METHODS

Species and areas

As reported by Jukema *et al.* (2013), data on more than 900 individuals of the reference species, the Eurasian Golden Plover (EGP), were collected in autumn and spring in staging areas in the north and the west of The Netherlands (52°N, 5°E) during the last twenty years of the 20th century by Joop Jukema (JJ) and Ton Pieters. During breeding in Iceland three EGP were checked in 2002.

Pacific Golden Plovers (PGP) from Siberia and Alaska were studied by JJ. In West-Siberia 24 PGP were caught on their nests in 1996 in Taymyr (Medusa Bay, 73°N, 81°E). In northeastern Mongolia (Mongol Daguur area, 49°N, 116°E) 294 PGP were caught in May 2005 staging on migration towards the West-Siberian breeding areas. In western Alaska 31 PGP were caught on their nests in 2008 and 2010 on Seward Peninsula (near Nome, 65°N, 166°W).

American Golden Plovers (AGP) were studied in the breeding area in western Alaska in 2008 and 2010 by JJ. On Seward Peninsula 13 AGP were caught on their nests. In Indiana, USA (Benton County, 41°N, 87°W), 96 AGP staging on migration towards Alaska were caught in April 2010. In their winter quarters in Uruguay 262 AGP were caught in the area of the Laguna Rocha (35°S, 54°W) in November 2010 and February and November 2011.

Between 1980 and 2000 non-systematic observations have been made on a few dozens of Grey Plovers (GP) caught in the north of The Netherlands. From 1999–2007 secondary moult was scored of 9 GP caught in August and September in Falsterbo, southern Sweden (55°N, 13°W) by Peter Olsson (PO). In 2008 and 2009 secondary moult was examined in 26 GP caught in December and January in Oman, Arabia (Barr al Hikman, 21°N, 59°E) by PO. By also using scattered information from other sources, in particular from Eddy Wymenga, a fairly complete account could be obtained.

Moult studies

With a focus on secondary moult, plovers were checked for the presence of secondaries that had not been renewed during the previous moult. This could provide information on the interruption of moult (suspended in case moult is resumed within the same moult cycle, or arrested if it will not be continued). For almost all birds that were caught in Alaska, Indiana, Uruguay, Falsterbo and Oman complete moult scores (Ginn & Melville 1983) were obtained for all the primaries and secondaries. Each secondary (numbered 1–11 from outermost to innermost) was scored on a 5-point scale where ‘0’ represents an unmoulted old feather and ‘5’ a fully developed new feather. More details on this procedure and on the catching techniques (Figure 2) are given by Jukema *et al.* (2013).

Migration patterns

General information on migration was gathered from standard works (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983, Piersma & Wiersma 1996, Byrkjedal & Thompson 1998, Johnson & Connors 2010). Additional information from specialist studies is added where possible.

RESULTS

Eurasian Golden Plover (EGP)

Secondary moult of EGP has been shown to be irregular, asymmetric and to involve only about half of the secondaries each year (Jukema *et al.* 2013). In contrast, primary moult was regular (inner to outer), symmetric and complete. The first primary and secondary moult was carried out in the second summer and autumn. When slightly older than one year, all primaries and only some outer and inner secondaries were replaced (Table 1). Primary and secondary moult of EPG largely overlapped, with primary moult starting somewhat earlier, during breeding. Secondary moult became arrested before November (Jukema *et al.* 2013) when primary moult was completed.

Pacific Golden Plover (PGP)

Large flight feather moult of PGP belonging to the breeding population of western Siberia proceeds approximately in the same way (Table 1). During spring migration in Mongolia 20 PGP (only 7% of all that were caught; $n = 294$) had not yet moulted their juvenile primaries and secondaries. Their age, almost one year old, was supported by the banding pattern of the outer retrices (Kinsky & Yaldwyn 1981). Apparently,

Figure 2. Catching American Golden Plovers in their winter area on the pampas of Uruguay with a traditional Dutch ‘wilsternet’. The net is well hidden, largely left of the picture, the ‘wilsterflapper’ stands in the back and, to attract the plovers there are two dozens of decoys in the front with their backs towards the net.

most one year old PGP do not return to their breeding area and probably stay in their winter quarters (Kinsky & Yaldwyn 1981, Byrkjedal & Thompson 1998). All other 274 PGP (93%) had renewed all primaries, but only about 50% of their secondaries in an irregular order and not strictly symmetrical between wings. These birds should have been almost two years or older, because as in EGP, the first moult of large flight feathers in PGP is delayed until the second summer, autumn or winter (Byrkjedal & Thompson 1998, Johnson & Connors 2010). All 24 breeding PGP in Taymyr displayed the same pattern: all primaries and about 50% of the secondaries renewed during the previous moulting cycle, indicating that they were at least two years old. Many of them (about 50%) had started already a new cycle of primary moult, but not yet secondary moult.

A different pattern was found in PGP belonging to the breeding population in Alaska (Table 1). All captured birds (n = 31) had a complete set of adult primaries, moulted in one cycle. In 26 PGP (84% of all) also a complete set of adult secondaries was observed, and in 5 PGP (16%) only the outer and inner secondaries were renewed. Not a single PGP was captured with a complete set of juvenile primaries and secondaries typical for yearlings. Unlike Siberian PGP, none of the breeding birds in Alaska had started a new cycle of primary moult. Assuming that the patterns of moulting in PGP are largely homologous to those in EGP, it is plausible that the 5 PGP that only renewed their outer and inner secondaries were about two years old, and all others at least three years. As sufficient information is lacking from the winter areas where moult proceeds, it cannot be excluded that some PGP, that are slightly older than one year, renew all secondaries. If so, the proportion of two-year old birds would be higher.

American Golden Plover (AGP)

Seemingly, AGP moult their primaries and secondaries in the same way as PGP. In Alaska there were almost no differences between AGP and PGP in the proportions of birds that had a complete set of adult secondaries and those that had renewed only a few. On the breeding grounds all AGP that were caught (n = 13) had a complete set of adult primaries, moulted in one cycle. In 9 AGP (69% of all) a complete set of adult secondaries was observed, and in 4 AGP (31%) only some of the outer and/or inner secondaries were renewed. None of these breeding birds had started a new cycle of primary moult. Patterns in the breeding area were highly similar

Table 1. Moulting strategies of large flight feathers, distances and migratory efforts in species and populations of tundra plovers *Pluvialis*.

	about half a year old	about 1.5 years old	≥ 2.5 years old
Eurasian Golden Plover **500–5000 km** **short flights**	no moult; no difference in colour and degree of wear	primary moult usually starts in breeding area; all primaries, only inner and outer secondaries	primary moult starts in breeding area; all primaries, 50% of secondaries
Pacific Golden Plover (Siberia) **6000–12,000 km** **Medium flights**	no moult; no difference in colour and degree of wear	wing moult usually starts during prolonged stay in winter area; all primaries, probably only inner and outer secondaries	primary moult starts in breeding area; all primaries, 50% of secondaries
Pacific Golden Plover (Alaska) **5000–10,000 km** **non-stop**	no moult; no difference in colour	primary and secondary moult in winter area, may start early during prolonged stay; all primaries, probably only and degree of wear	primary and secondary moult after return in winter area; all primaries, all secondaries inner and outer secondaries
American Golden Plover (Alaska) **10,000 km** **non-stop**	primary and secondary moult fairly late in winter area; all primaries, only inner and outer secondaries	primary and secondary moult after return in winter area; all primaries, all secondaries	primary and secondary moult after return in winter area; all primaries, all secondaries
Grey Plover **4000–14,000 km** **variable**	no moult; no difference in colour and degree of wear	moult tends to start early; all primaries, inner and outer or all secondaries	moult tends to start later; all primaries, various or all secondaries

to those during spring migration. All birds that were caught in Indiana ($n = 96$) had a complete set of adult primaries, moulted in one cycle. In 85 AGP (89% of all) a complete set of secondaries was observed, and in 11 AGP (11%) only some of the outer and/or inner secondaries were renewed. The number of secondaries that had been replaced varied between individuals, but remarkably, renewal in left and right wings of all 11 individuals was symmetric (Table 2).

In contrast to all other *Pluvialis* species, the first moult of the large flight feathers in AGP occurs when they are about half a year old (Jukema *et al.* 2011) and includes all primaries and usually some outer and inner secondaries. In Uruguay 38 (69% of all) juveniles that were caught in November ($n = 55$) had started primary moult already, but none had begun to renew its secondaries. All juveniles ($n = 36$) that were caught in February had completed (or almost completed) moult of their primaries. Among these, 27 (75%) had renewed some of their inner and/or outer secondaries, and most

Table 2. Moult scores of the secondaries of 11 American Golden Plovers (almost one year old) that were caught during spring migration in Indiana. The other 85 AGP (almost two or more years old) caught at the same place and time had all their secondaries renewed.

Left wing	Right wing
50000000004	50000000004
55000000000	55000000000
55550000000	55550000000
55000000000	55000000000
55000000005	55000000005
55555055555	55555005555
55000000005	55000000005
55000000005	55000000005
55500000555	55500000555
50000000055	50000000055
55000000005	55000000005

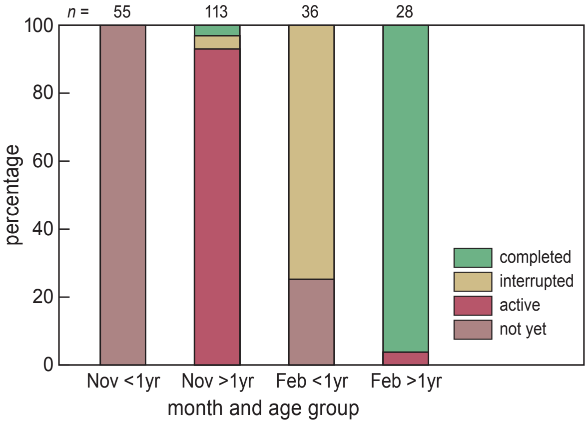

Figure 3. Secondary moult in November and February of American Golden Plovers aged <1 year and >1 year in Lagoon Rocha, Uruguay.

probably arrested moult up to the following cycle (Figure 3). The other 9 birds had not yet started secondary moult. It seems plausible that these do not continue wing moult as they have to get ready for migrating north. Most (94%) older AGP were actively moulting their secondaries in November and almost all (96%) had completed their secondary moult in February (Figure 3). Yet, the order of secondary moult appeared to be irregular as in the other tundra plovers (Figure 4). Secondary moult scores of the two wings were symmetric in only 22% of all AGP during active moult, but in 97% when moult was interrupted. The data from Uruguay showed that breeding AGP that possess a complete set of fresh primaries and a small number of renewed secondaries were only one year old (Table 1). Apparently, quite a number of such birds return to the breeding grounds. Breeding AGP that possessed a complete set of fresh secondaries were two or more years old. This contrasts with PGP from Alaska. PGP, both in the group with partial secondary moult and in the group with complete secondary moult, were one year older (two and three or more respectively).

Grey Plover (GP)

Non-systematic observations on secondary moult of dozens of GP that were caught for ringing in The Netherlands were in agreement with the general pattern that was known from the EGP: incomplete, irregular and lacking in the first winter. Boere (1976) also reported interrupted moult of the secondaries in GP from the Wadden Sea area in The Netherlands. Secondary moult may be suspended during the winter, resumed in early spring, and finally arrested before completion, as could be deduced from a GP that was caught in November (3 full grown new secondaries, all others old) and retrapped in March (6 full grown new secondaries, all others old). Boere's data also show that the first primary moult (and most likely also secondary moult) in young GP (about one year old) may start in July, well before the older (two or more years old) birds in August.

Among the adult GP that were caught at Falsterbo Bird Observatory in August and September, two (22%) had not started primary or secondary moult, five (56%) had started to moult their primaries but not yet secondaries, and two (22%) had renewed all primaries and secondaries. From the latter two, one was evidently a second calendar-year bird. Quite a number of juveniles were caught (*n* = 46) but none had initiated wing moult.

GP caught in Oman in December and January (*n* = 28) had completed or almost completed primary moult. Progress of secondary moult was much more variable: 14/26 (54%) had renewed all secondaries, 5/28 (18%) had interrupted secondary moult and 7/26 (27%) were still moulting their secondaries. In GP that did not complete secondary moult, total secondary moult score was on average about 60% of the maximum score. Irregular moult was seen in 11 out of these 12 GP. Two GP caught in Oman were evidently less than two years old and both had renewed all secondaries. None of the juveniles that were caught in Oman (*n* = 4) had started to moult primaries or secondaries.

Figure 4. Irregular secondary moult in a two or more years old American Golden Plover caught in November in Uruguay. Secondary moulting score is 10000550012, but S1 (left) and S10 and S11 (right) are not visible. Moulting started in the middle (S6 and S7) and then began both with inner (S11 and S10) and outer (S1) secondaries.

Interrupted and irregular secondary moult was also observed in some dozens of GP – though not in all – caught in Tunisia in January and February 1984 and in Guinea-Bissau, western Africa in December 1986 (E. Wymenga pers. comm.). In GP the order of secondary moult is irregular, in any case, but there is *no consistent pattern* in timing and completeness. The latter is undoubtedly due to the rather small set of heterogeneous data from various age classes, regions and moult stages. Yet, the data suggest that one year old GP moult earlier than the older GP. In addition, some, perhaps many adult (including one year old) GP tend to renew all secondaries. Other GP probably renew only part of the number of secondaries, in one year old GP especially the outer and inner ones (Table 1).

DISCUSSION

Timing and pattern of secondary moult

Table 1 summarizes the range of moulting strategies of *Pluvialis* plovers. Most species of tundra plovers do not renew their large wing feathers before they are one year old. The AGP is the only species that deviates from this general pattern. It usually begins to moult at an age of about 6 months (Jukema *et al.* 2011). This first wing moult of AGP starts one or two months *later* than wing moult begins in the older generations, possibly because juveniles arrive later in the winter quarters than older AGP. In contrast, in at least the PGP from Alaska and the GP the first wing moult at an age of about one year usually begins some time *before* the older generations start wing moult. Many of these younger birds are able to moult early because they do not participate in breeding and some might have stayed in the winter area. In the EGP and AGP only the outer and inner secondaries are renewed during their first wing moult. Although conclusive evidence from the moulting areas is lacking, we suspect the same (homologous) pattern in PGP, both from Siberia and Alaska. Some data (from Falsterbo and Oman) suggest that some, perhaps many, GP diverge from this by moulting all their secondaries at the time of their first wing moult.

In EGP and PGP from Siberia about half of the secondaries are renewed in subsequent years. In PGP from Alaska and AGP all secondaries tend to be renewed during their second and later wing moults. GP do not show a consistent pattern. Some of them seem to have an incomplete secondary moult, whereas others renew all. In all species of tundra plovers the order of secondary moult is irregular, and, especially in the EGP, moult of the two wings is often asymmetric. It is remarkable that within a group of closely related species such large differences in moulting strategies occur, but it is even more remarkable that such differences occur within one single species, the PGP.

Flight distance and fat storage

EGP have been suggested to be able to afford incomplete replacement of secondaries because of their short flight distances during migration: this would not lead to much wear and tear, nor do these flight distances necessitate newly moulted flight feathers (Jukema *et al.* 2013). Distances between breeding areas and winter quarters (Figure 1A) range between a few hundreds up to about 5000 km in a straight line (estimated from the information by Byrkjedal & Thompson 1998 – as for the other distances below), but the daily movements are not very extensive. This is reflected by changes in body mass that may indicate changing fuel loads, but also other physiological transformations (Piersma 1998). Preceding spring migration, body mass increases by about 25% but fat mass remains low (about 10% of body mass). Instead, marked changes occur in protein mass (Piersma & Jukema 2002). Yet, EGP are able to store fair amounts of fat (25% mass increase, up to 40% in the absence of raptors), but this occurs in late autumn and winter as an insurance strategy to cope with bad foraging conditions (Piersma *et al.* 2003).

PGP from Siberia travel long distances (ranging between about 6000 and 12,000 km in a straight line) from their breeding quarters to southeastern Asia (Figure 1B), including the Indonesian Islands. This seems to contrast with the EGP. However, PGP migrate transcontinentally and along the Asian coast (East Asian-Australasian flyway), mainly over land. They are able to stage at short intervals (Johnson & Connors 2010). This kind of migration is not necessarily very different from the wandering habits of EGP, that may fly considerable distances each year, but within a comparatively restricted area (Byrkjedal & Thompson 1998). PGP from Siberia are preparing to make longer flights than EGP. Preceding spring migration PGP store more fat than EGP. In Mongolia their body mass may increase by 3 g per day, about 40% in two weeks (total fat mass is then about 25% of their lean mass) before their departure to the Siberian breeding grounds, about 3000 km away (Wijmenga *et al.* 2011).

GP may also travel long distances from their breeding areas in the extreme Arctic via the coastal areas of the northern and southern hemisphere (Figure 1D), up to southern Africa and northern Australia (ranging between 4000 and 14,000 km in a straight line). As for

PGP from Siberia, they mainly travel along coasts, and, when passing suitable habitats, they may be able to stage and forage at relatively short intervals. Yet, they seem to be prepared to make rather long flights. Body mass of GP wintering in Britain increases by about 40% at the time they depart to their breeding area (Serra *et al.* 2006). In South Africa there is a body mass increase of about 45% before northward departure occurs (Serra *et al.* 1999). GP wintering far south move so fast from their breeding area to the winter quarters that hardly any time is left for staging. For instance, in South Africa GP arrive in September, shortly after the end of breeding (Serra *et al.* 1999). Most probably, these journeys also include one or more fairly long non-stop flights.

Migration habits of the PGP from Alaska are still more exhausting. Geolocators have revealed that these birds make long-distance flights (Johnson *et al.* 2011, 2012) requiring extreme efforts comparable to those documented for Bar-tailed Godwits *Limosa lapponica baueri* (Gill *et al.* 2009, Battley *et al.* 2012) and Ruddy Turnstones *Arenaria interpres* (Minton *et al.* 2010). PGP from Alaska make two or three very long non-stop flights (each 5000–10,000 km lasting 3–7 days). Some of them winter on the Hawaiian Islands and directly return to Alaska in spring, others winter in the southwestern Pacific up to Australia and return via Japan to Alaska (Figure 1B). They certainly need a considerable amount of fuel to make these flights. In Bar-tailed Godwits, for example, fat mass raises up to 120% of lean mass in juveniles departing from Alaska, and to 75% of lean mass in adults departing from New Zealand (Piersma & Gill 1998). In PGP wintering on the Hawaiian Islands fat stores rise to almost 50% of the lean mass before departing north (Johnson *et al.* 1989). It is quite likely that fuel loads are still higher in PGP departing from Alaska to the southwestern Pacific Islands, but this has to be verified.

AGP also make very long non-stop flights (Johnson & Connors 2010). In autumn they tend to depart in huge flocks from the eastern coast of Canada for one single flight over the Atlantic to their winter area in Argentina (Figure 1C), a distance in the range of 10,000 km. Juveniles and some older birds may fly over land. In early spring all birds return over land (midcontinental flyway) to Alaska and Canada (Johnson & Connors 2010). Unfortunately no data are available on fat stores when AGP depart from Canada. Data from Uruguay give some hints on the abilities of AGP (Figure 5). The data from November suggest that lean mass of adults is about 120 g and of juveniles about 110 g. In February, at the time that some birds are ready to depart (over land), the heaviest adults have gained about 50% extra mass and the heaviest juveniles about 55%. We suspect that mass increase is still higher before their departure from Canada.

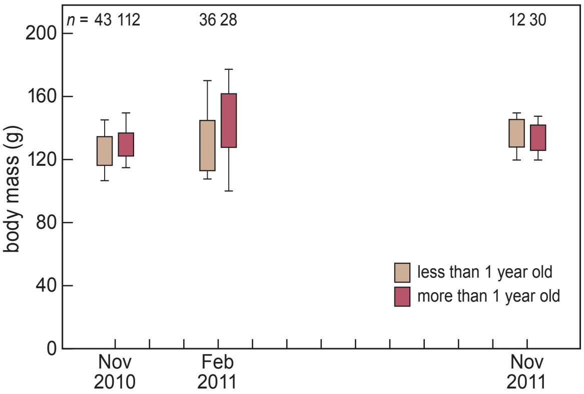

Figure 5. Body mass of adult and juvenile American Golden Plovers caught in Uruguay. Vertical lines represent the full range of measurements, boxes represent averages ± 1 SD.

Wing quality

Long non-stop flights require appropriate wings, not only to bridge the distance, but also to bear the extra load of fat (e.g. Norberg 1995, Bowlin & Wikelski 2008). For that reason species that have to make such flights need extra wing surface to carry this load. Wing loading is defined as (body mass)/(wing surface). We assume that, for birds with the same wing shape, wing surface equals the square of wing length multiplied by a constant factor C. Then, the differences between wing loadings of lean birds of the four species can be calculated. Lean mass is 190 g for EGP, 110 g for PGP, 120 g for AGP and 220 g for GP (Johnson *et al.* 1989, Serra *et al.* 1999, 2006, Piersma & Jukema 2002, Wijmenga *et al.* 2011, this study). Wing length is taken to be 186 mm for EGP, 164 mm for PGP, 179 mm for AGP and 199 mm for GP (data from Byrkjedal & Thompson 1998). Wing loadings in lean EGP ($5.5/C$ kg/m^2) and GP ($5.6/C$ kg/m^2) appear to be almost identical, but wing loading in lean PGP ($4.1/C$ kg/m^2) is about 25% lower and in lean AGP ($3.7/C$ kg/m^2) even 33%. However, $3.7/C$ kg/m^2 might be an underestimate, as AGP wings are slender in comparison with the other species (Byrkjedal & Thompson 1998). Thus, both PGP and AGP seem to have extra wing capacity for fuel transportation. Our own data (Jukema *et al.* unpubl. data) suggest that this holds stronger for PGP from Alaska than for the Siberian PGP.

Long distance flights also demand a complete set of strong flight feathers. It could be risky to renew them *just before* departure. This is especially relevant for Arctic breeders that are faced with narrow time schedules (e.g. Holmgren & Hedenström 1995, Barta *et al.* 2008, Buehler & Piersma 2008, Conklin & Battley 2012, Dietz *et al.* 2013). For them fuelling may have a higher priority. EGP were observed to start wing moult in their breeding area and to suspend moult during migration (Jukema *et al.* 2013). Commonly, however, this species does not breed under extreme Arctic conditions, and migrates over short or moderate distances. Also, 40–50% of the PGP in Siberia start primary moult in their breeding area (Byrkjedal & Thompson 1998), although breeding conditions may be harsher than in EGP. But again they do not have to make long non-stop flights after breeding. Most of the GP that were caught in August and September in Falsterbo had suspended primary moult. This suggests that these also started wing moult in their breeding area. In contrast, GP that migrate to the tropics and further south postpone wing moult until they arrive in their winter quarters (e.g. Serra 1999). Breeding conditions and migratory efforts in some GP populations must be in the same range as in PGP from Siberia, but in some other GP populations migration efforts seem to approximate those of PGP and AGP from Alaska.

Thus, species and populations, that fly short or moderate stretches after breeding, tend to start wing moult in their breeding area *before* fall migration. For species and populations that have to make long non-stop flights there is no convincing evidence that wing moult starts in the breeding areas. AGP and PGP from Alaska (and GP wintering in South Africa) begin and complete wing moult *after* fall migration in their winter quarters (Johnson & Johnson 1983, Barter 1988, Serra 1999, Johnson & Connors 2010, Jukema *et al.* 2011). Although it is totally clear that there is not enough time in the breeding areas for pre-migratory fattening *and* wing moult, it is surprising that the longest non-stop flights (during autumn migration) are made when flight feather quality is lowest. Only slightly shorter flights during northward migration have been found in other marathon migrants, such as Bar-tailed Godwits (Gill *et al.* 2009, Battley *et al.* 2012). Possibly, the recovery of the very longest non-stop flight concluding northward migration is incompatible with the preparations for breeding in an Arctic environment. Thus, wing moult in late autumn and winter should not only be considered in relation to spring migration, but more importantly, as a requirement for the return flight in early autumn next year. An early arrival in the wintering area, and especially a southern wintering area where environmental conditions do not deteriorate rapidly with the onset of winter, might enable birds to improve their body state for the following breeding cycle, for instance by being able to spend much time for moulting and thus to produce stronger flight feathers (e.g. Serra 2001, Conklin & Battley 2012, Dietz *et al.* 2013).

Age at first breeding

Age of first breeding should be interrelated with migration and moulting schedules. AGP generally return to their breeding areas when they are almost one year old, and at least some of them attempt to breed (Johnson & Connors 2010, this study). One year old EPG and GP often return to their breeding grounds, but there is no agreement about their readiness to breed (e.g. Glutz *et al.* 1975, Parr 1980, Cramp & Simmons 1983, Johnson & Connors 2010). Some one year old PGP from Alaska also return (O.W. Johnson pers. comm.), but many stay in their winter quarters (Hawaiian and other Pacific islands). PGP from Siberia seem to return when they are almost two years old (this study) or older. Thus, it is remarkable that AGP that have to make about the longest journey to reach their winter quarters return in their first year. Maybe, the conditions in their winter quarters between April and August are unsuitable for them to stay. It is plausible that their early wing moult at an age of about 0.5 year old has evolved as an adaptation to successfully make the return flight to the breeding area and/or – more importantly – to be able to make the long non-stop flight after their first attempt to breed.

Irregular moult

The irregular and incomplete moult of secondaries in tundra plovers is peculiar. During their first wing moult the outer and inner secondaries are renewed. During later moults a few or all secondaries are renewed, but always in a non-systematic order. This does not seem to be the most effective way of moulting for long distance migrants. The character is known from some other related species, such as Northern Lapwings *Vanellus vanellus* (see Jukema *et al.* 2013) but as far as we know not yet in their closest relatives according to DNA studies (Baker *et al.* 2007, Fain & Houde 2007): oystercatchers, stilts and avocets. In Eurasian Oystercatchers *Haematopus ostralegus* secondary moult seems to proceed regularly (P. Olsson unpubl. data, K. Oosterbeek pers. comm.). Probably this is a fairly primitive character that is still retained, also in the species and populations of tundra plovers that make long non-stop flights.

Originally irregular moult may have been linked to conditions that did not force the bird to renew all its secondary flight feathers every year. Only those feathers that were heavily worn had to be moulted. Such a strategy could improve fitness by a lower rate of food conversion, but is only possible as long as movement patterns are relaxed. This strategy is exemplified by the population of EGP that breed in England, Ireland and Scotland. These birds winter very close to the breeding area and rarely leave the British Islands (Cramp & Simmons 1983). Long-distance migrants had to evolve a more complete moulting pattern. Both the AGP and the PGP from Alaska have their first (incomplete) secondary moult by the time they are ready to breed. In subsequent years they renew *all* secondaries. A long stay in (sub)tropical areas might be an additional factor for the need of a more complete moulting pattern, as heavy sun irradiation might have harmful effects on the flight feathers (Johnson & Johnson 1983).

Conclusion

In conclusion, our prediction that annual replacement of secondaries in tundra plovers is related to migration distance appears to hold up. However, total migration distance is possibly not the most important factor enforcing complete secondary moult. Rather, it is the length of the non-stop flights that have to be made that are critical. These include not only the flights that take place immediately after moult completion, but also flights occurring just before the next moulting cycle. Remarkably, these latter flights appear to be the longest. The evolution of an extra wing moult in 0.5 year old AGP enables these long-distance migrants to participate in the first *and* following breeding opportunities.

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SAMENVATTING

Vogelveren zijn kwetsbaar en moeten in de loop van een vogelleven geregeld worden vernieuwd. Dit ruiproces kost energie en tijd, een proces dat in de loop van de tijd wordt bijgestuurd door natuurlijke selectie. Een vogel ruit daarom zijn veren vaak genoeg, maar niet vaker dan strikt noodzakelijk is. Bij Goudplevieren *Pluvialis apricaria* hebben we onlangs aangetoond dat de rui van de armpennen (ook wel kleine slagpennen genoemd) onvolledig, onregelmatig en niet symmetrisch tussen beide vleugels verloopt. We veronderstellen dat dit mogelijk is doordat de vogels op hun trek geen lange dagtrajecten afleggen en de afstand tussen broedgebieden, pleisterplaatsen en wintergebieden niet groot is. Als dit idee klopt, kunnen we verwachten dat bij nauw verwante soorten die verder trekken en/of langere trajecten in één keer afleggen, de rui van de armpennen vollediger en misschien ook regelmatiger en meer symmetrisch is dan bij de Goudplevier. We hebben dit getest door ruigegevens te verzamelen van Aziatische Goudplevieren *P. fulva* uit Siberië en Alaska, Amerikaanse Goudplevieren *P. dominica* uit Alaska en Zilverplevieren *P. squatarola* van verschillende herkomst. De gegevens zijn afkomstig uit de broedgebieden (klein deel), pleisterplaatsen (Mongolië en Indiana in de Verenigde Staten) en overwinteringsgebieden (Uruguay). De manier waarop vogels van deze populaties/soorten hun armpennen ruien, hebben we vergeleken met hun trekpatronen. Het verband dat we verwacht hadden, blijkt inderdaad te bestaan. Aziatische Goudplevieren uit Siberië en (sommige) Zilverplevieren hebben ongeveer hetzelfde ruipatroon als de Goudplevier. Weliswaar liggen hun wintergebieden veel verder van de broedgebieden weg dan bij de Goudplevier, maar de trekroute loopt hoofdzakelijk over land. Ook worden er meestal geen erg lange trajecten aan één stuk gevlogen. Daarentegen is bij de Amerikaanse Goudplevier de rui van de armpennen vanaf de tweede ruicyclus volledig en bij de Aziatische Goudplevier uit Alaska vrijwel volledig. Zoals verwacht leveren deze vogels een veel grotere inspanning dan de Goudplevier op de trek tussen hun broed- en overwinteringsgebied. Voor beide plevieren uit Alaska geldt dat zij enorme trajecten aan één stuk (5.000–10.000 km gedurende 3–7 dagen) afleggen. De Amerikaanse Goudplevier is bovendien de enige soort die in de eerste winter al sommige van zijn armpennen ruit. Vaker dan bij de andere soorten komen één jaar oude vogels van de Amerikaanse Goudplevier ook al tot broeden. Ondanks alle verschillen zijn er treffende overeenkomsten in de rui van de armpennen tussen de vier soorten plevieren. Die verloopt onregelmatig, terwijl bij de eerste ruicyclus van de armpennen alleen de buitenste en binnenste pennen worden vernieuwd. Wij betogen dat onvolledige en onregelmatige rui de oorspronkelijke toestand is binnen deze groep. De volledige vernieuwing van de armpennen bij de Aziatische Goudplevieren uit Alaska en de Amerikaanse Goudplevieren zou dan een aanpassing zijn die later in de evolutie is ontstaan voor de extreem lange vluchten. Een regelmatige rui, zoals we bij veel andere steltlopers aantreffen, zou dan te beschouwen zijn als een perfectionering van deze aanpassing.

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