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Differential migration of juvenile and adult Grey Plovers *Pluvialis squatarola* at the mouth of the Vistula River, Poland

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Ringing data of 130 juvenile and 65 adult Grey Plovers caught between mid-July and mid-October at the mouth of the Vistula River, Poland, in the years 1983–1996 allowed timing and description of a differential migration between these two age classes. Body mass did not vary during the whole period of passage in adults, averaging relatively low values, while an increase in mass towards the end of migration was observed in juveniles. An age-related site exploitation was suggested to explain different daily trapping patterns. Most of the migrating adults had not yet started primary moult, and only 11% were in, or very close to, suspension stages of innermost feathers.

1. Introduction

Adult arctic waders generally leave breeding grounds before juveniles. This behaviour generates patterns of differential migration (*sensu* Gauthreaux 1982, Terril & Able 1988), with adults passing through particular stopover sites earlier than juveniles (e.g. Gromadzka 1987). Differences in timing are associated, at least in some species, with age-specific migration routes, which are usually shorter in adults (Stanley & Minton 1972, Wilson et al. 1980). Differential migration has generally been interpreted as an evolutionary product to avoid intra-specific competition at stopover sites, although the role and importance of intra-specific competition on staging migrants has never been ascertained (Berthold 1996).

Along the Atlantic coast of Europe, the autumn passage of adult and juvenile Grey Plovers *Pluvialis squatarola* in two distinct waves is well known. Adults migrate through northern Europe from late July to August, with females preceding males; juveniles appear from late August–September and probably peak in October (Kube & Struwe 1994, Meltofte 1993, Meltofte et al. 1994). Nevertheless, detailed information on timing of migration, as well as physiological and moult conditions, was not available for staging sites located north of the main wintering and/or moulting areas. A long-term ringing project carried out in the southern Baltic, just north of the regular winter range, provided data to be analysed to fill this gap.

2. Study area and methods

Waders have regularly been ringed and studied at the mouth of the Vistula River (54°21´N, 18°57´E), in northern Poland, since the early

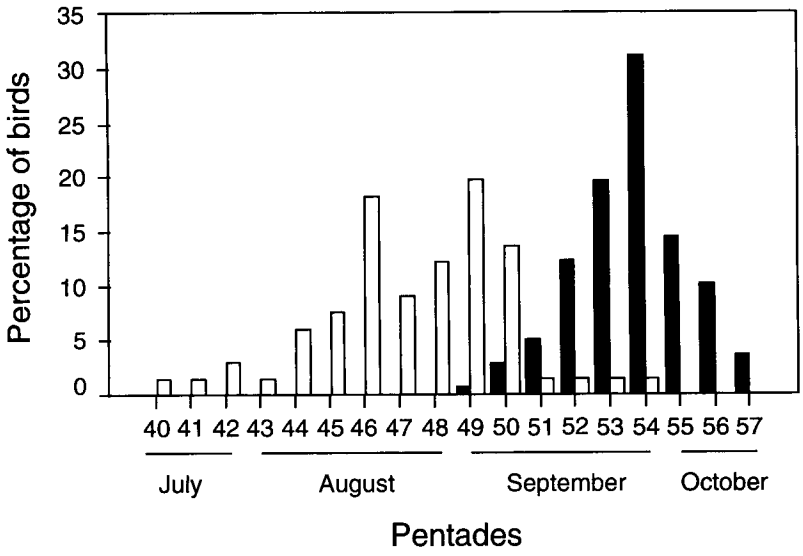

Fig. 1. Seasonal trapping distribution of adult (n = 65; open bars) and juvenile (n = 130; filled bars) Grey Plovers at the mouth of the Vistula River, Poland. Pentade 40 = 15–19 July, 57 = 8–12 October.

1960s. Ringing seasons generally spanned from mid-July to the end of September. Waders were trapped with walk-in traps, Ottenby type, set along sandy shores facing the sea or the river mouth; the traps were checked daily every two hours, from dawn to dusk (cf. Gromadzka 1981, 1987). Despite the trapping equipment being specially designed for small *Calidris* species, which were predominant at the mouth of the Vistula River during the study period, larger waders occasionally entered the traps, too.

Grey Plovers do not occur at the mouth of the Vistula in large numbers and usually only single birds or small flocks stop there. Occasionally, flocks of some hundreds have been observed, e.g. mid-October 1978, when about 500 juveniles were found together with about 600 juvenile Dunlins *Calidris alpina*. Data from the period 1983 to 1996 were used in this study.

Grey Plovers were ringed, weighed with Pesola spring balances (accuracy: 2 g), and measured according to standard techniques (cf. Gromadzka & Przystupa 1988). Wing and tarsus plus toe lengths were taken to the nearest mm, total head, bill and tarsus lengths to the nearest 0.1 mm. Primary moult was recorded giving the following scores: 0 = old feather, 1 = feather missing or in pin, 2–4 = progressive stages of growth, 5 = full grown new feather (Ginn & Melville 1983). Birds were aged according to plumage characters (Prater et al. 1979).

Where not otherwise stated, data were pooled into 5-day periods (pentades) numbered from the beginning of the year (Berthold 1973), and covering the period 15 July to 14 October (pentades: 40–57). Pentades 40–44 were pooled for body mass analysis, because few birds were trapped so early in the season. Linear regression analyses were performed taking days, numbered from 1 July, as the independent variable. For daily trapping patterns, birds were grouped into eight two-hour classes, from 5h to 21h.

3. Results

3.1. Trapping patterns

Between 1983 and 1996, 130 juveniles and 65 adults were ringed. Only one adult (2%) and eight juveniles (6%) were caught twice at the study area within the same migration season, at one- (5 juveniles and 1 adult), two- (1 juvenile) and three- (2 juveniles) day intervals from capture. The seasonal trapping pattern showed a clear segregation between the passage of adults and juveniles (Fig. 1). The first adults were already on route at the beginning of the study period (mid-July). Their passage showed a bimodal distribution with peaks on 14–18 August (pentade 46) and 29 August–2 September (pentade 49), followed by a rapid decrease.

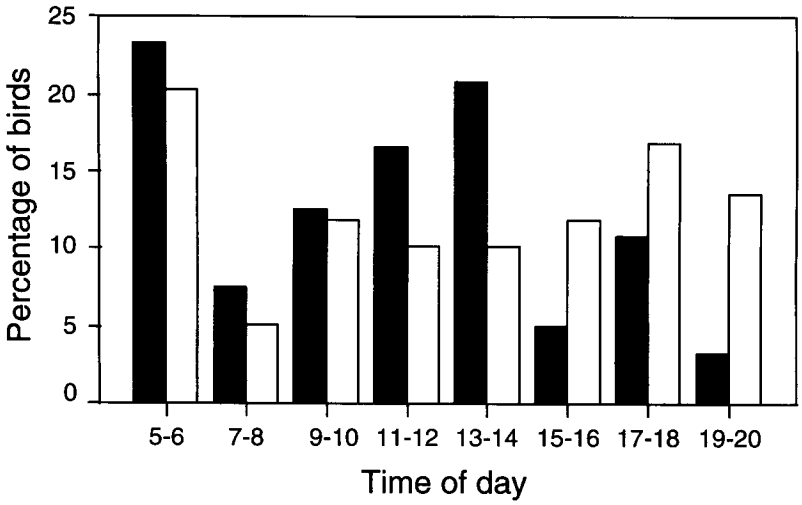

Fig. 2. Daily trapping pattern of adult (n = 65; open bars) and juvenile (n = 130; filled bars) Grey Plovers at the mouth of the Vistula River, Poland.

Juveniles were recorded from late August to mid-October, showing a single peak on 23–27 September (pentade 54).

The daily trapping patterns of juveniles and adults differed significantly (Fig. 2; Kolmogorov-Smirnov test, $z = 1.46$, $p < 0.03$). Adult trapping distribution did not differ from random, maintaining a rather constant trapping rate in the course of the day, while that of juveniles did ($\chi^2 = 31.4$, d.f. = 7, $p < 0.001$). Nevertheless, both age classes showed a maximum just after dawn (5–6 a.m.), followed by a minimum at 7–8 a.m. The number of trapped juveniles then showed a steady increase, reaching a second peak in the early afternoon, followed again by a sharp decline. Subdividing the trapping season into two parts, before 27 and after 28 September (last day of pentade 54 and first day of pentade 55, see next paragraph), the daily patterns of early and late juveniles were not different (Kolmogorov-Smirnov z test).

3.2. Biometrics

Wing, total head and bill lengths were significantly different between the two age classes (Table 1). Within each age class, no linear measurements significantly correlated with time expressed by days. The migration season of adults was divided into two periods, up to 23 August (last day of pentade 47) and from 24 August (first day of pentade 48) onwards, to test the presence of biometrically different groups in the two observed migration waves (Fig. 1). Mean wing lengths of the two samples were significantly different (first period: mean = 198.7, S.D. = 3.9, n = 29; second period: mean = 203.1, S.D. = 6.5, n = 20; t-test = 2.92, d.f. = 47, $p < 0.005$).

Adult body mass values did not vary significantly during their period of passage (linear regression of mass on days, $F_{1,61} = 0.76$, N.S.), and the same applied to juveniles in the earlier part of their migration period, from 29 August (first day of pentade 49) to 27 September (last day of pentade 54; linear regression of mass on days, $F_{1,88} = 0.36$, N.S.) (Fig. 3). Among juveniles, a significant body mass increase was observed regressing mass on days from 23 September (first day of pentade 54) to the end of the season ($r^2 = 0.43$, $F_{1,80} = 59.92$, $P < 0.0001$), when birds averaged about 40 g more than in the first period.

During most of the migration season (up to 27 September, pentade 54) adults were about 6 g heavier than juveniles ($F_{1,151} = 4.8514$, $p < 0.03$), averaging 174.2 g (S.D. = 15.6, range 142–222, n = 62) and 167.9 g (S.D. = 18.3, range 112–222, n = 91) respectively. Later on, from 28 September onwards, after juveniles started gaining mass, they became heavier than adults ($F_{1,98} = 61.185$, $p < 0.001$; juv. mean = 205.5 g, S.D. = 24.4, range 163–276, n = 38).

Over the whole trapping season, mean body masses did not vary in the course of the day, both in juveniles and adults (one-way ANOVA).

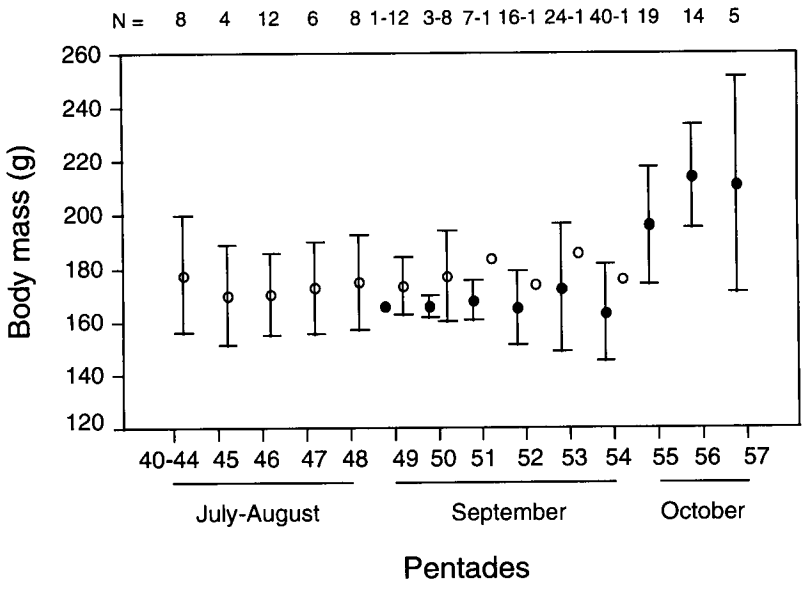

Fig. 3. Seasonal body mass variations of adult (open dots) and juvenile (solid dots) Grey Plovers at the mouth of the Vistula River, Poland. Means, standard deviations and sample sizes are indicated. Pentade 40 = 15–19 July, 57 = 8–12 October.

3.3 Primary moult

All adults (n = 65) were checked for primary moult. Among these, 58 (89%) had not started to moult, five (8%) were in active moult and two (3%) were in suspended moult stages (Table 2). No juveniles showed primary moult.

4. Discussion

A clear pattern of differential migration with a shift in the passage of adults and juveniles was identified, supporting previous information obtained by census data (Meltofte 1993, Kube & Struwe 1994, Meltofte et al. 1994).

Table 1. Biometrics of juvenile and adult Grey Plovers ringed at the mouth of the Vistula River in the years 1983–1996.

	Age	Mean ± S.D.	Min–Max	n	t	d.f.	p
Wing (mm)	Juv.	196.0 ± 5.7	182–224	128	4.7	175	0.001
	Ad.	200.5 ± 5.5	188–215	49			
Total head (mm)	Juv.	64.9 ± 2.0	60.0–70.0	122	4.3	164	0.001
	Ad.	66.5 ± 2.3	59.5–70.0	44			
Bill (mm)	Juv.	28.3 ± 1.2	25.8–32.0	127	[1]5.0	95.7	0.001
	Ad.	29.4 ± 1.7	26.0–34.0	64			
Tarsus+toe (mm)	Juv.	81.4 ± 3.9	72–87	14	1.0	25	0.3
	Ad.	82.8 ± 2.8	76–86	13			
Tarsus (mm)	Juv.	47.0 ± 2.0	42.1–51.1	34	1.8	59	0.07
	Ad.	48.0 ± 1.9	43.4–52.3	27			
Body mass (g)	Juv.	179.0 ± 26.5	112–276	129	[1]51.5	181.5	0.12
	Ad.	174.2 ± 15.6	142–222	62			

[1] t-test calculated for unequal variance

The daily trapping patterns showed a different use of the area by adults and juveniles. Our data cannot explain whether the hourly trapping rates may be considered an indication of a different feeding behaviour, site prospecting strategy, or simply a differential timing of arrival of newly landed birds, but the existence of age-related migration strategies connected with different site searches, selection and use has been suggested for other waders (Rösner 1990, 1997, Townshend & Evans 1988). In particular, the presence of a peak of activity in the middle of the day could indicate more persistent attempts by juveniles to exploit the feeding resources of the site; adults, conversely, seem to give up sooner and leave. Such a strategy on behalf of juveniles would result in slower rate of migration speed as compared with adults, which is indeed supported by more local retraps.

Adults did not show any seasonal variation in body mass, maintaining relatively low and constant mean values through time (Fig. 3). With respect to Grey Plovers staging at the Wash, England, in August, in Morocco in September, and at the Banc d'Arguin, Mauritania, in October, Polish birds were, respectively, 23%, 12% and 18% lighter (Dick & Pienkowski 1979, Johnson 1985, Lesink & Meininger 1990). Hence, if an increase in pre-migratory body mass on the breeding grounds or in their close proximity is assumed — for which no information is available — this result would suggest that adults stopping at the mouth of Vistula River are newly landed birds, perhaps at their first stopover from the breeding grounds, after a long non-stop flight. On the other hand, a route covered with short flights and frequent stopovers, which would, theoretically, imply carrying low energy loads under an optimal migration perspective (Alerstam & Lindström 1990), can probably be excluded considering how the species behaves in other parts of the east Atlantic flyway (Branson & Minton 1976, Summers & Waltner 1979, Zwarts et al. 1990).

The juvenile seasonal body mass pattern resembled that of adults for most of the migration season, but showed a sudden change during the final period (October) when juveniles carrying large energy reserves appeared (Fig. 3). Towards the end of the passage, the need for storing energy for a further migration step — because of its endogenous control (Berthold 1975, 1984) — could be strong enough to force birds to start mass gain independently of latitude and/or trophic quality of the site they have reached. This fact should be reflected in longer stays and, probably, different daily rhythms of activity. However, our data failed to show such hourly differences between early and late migrants, probably because no really suitable spots to replenish energy reserves were available and, consequently, juveniles did not stay long after they had tested the quality of the site.

The onset of primary moult on the breeding grounds (Cramp & Simmons 1983, Hötker 1995) and the arrival at the main moulting areas of birds showing the innermost 1–3 primaries in suspended moult stages were already known (Boere 1976, Branson & Minton 1976). Five out of 10 males (50%) and 1 out of 14 females (7%) ringed on the Taimyr Peninsula between 28 June and 20 July 1989–91 were in active primary moult (Hötker 1995). Similarly, at Sibiryakov Island (72°44N, 79°08E) in summer 1990 and at the mouth of the Pyasina River (Taimyr, 74°07N, 86°52E) in 1991, five males (19%) out of 26 trapped, whereas none of the 29 females, were moulting at the same time (P. Chylarecki & A. Sikora pers. comm.). On the Yamal Peninsula, none of the 90 breeders caught between 21 June and 20 July in 1990–1995 was in active moult, possibly because most birds were ringed around the end of June and the beginning of July (V. Ryabitsev pers. comm.). On Taimyr, for birds selected after 14 July, when the first moulters were found, the proportions of moulting birds in the two samples were 38% (n = 18) and 27% (n = 19), respectively. Furthermore, these

Table 2. Trapping dates and primary scores (see Methods) of five active and two suspended moulting adult Grey Plovers. Out of 65 adults captured, 58 had not started primary moult.

	Date	Primary score
1	9 August	5440000000
2	14 August	4000000000
3	14 August	5540000000
4	15 August	4400000000
5	25 August	4000000000
6	25 August	5500000000
7	6 September	5550000000

data suggest that the majority of Grey Plovers found in suspended or active moult during the first part of the post-breeding migration are males.

Frequencies of birds in suspended or active moult at the mouth of the Vistula River (11%) were lower than those observed in Taimyr or at the Wash. Different moult strategies at a population level can hardly be considered to explain this pattern, as the onset of primary moult in males seems a widespread phenomenon throughout the breeding range. An alternative hypothesis might involve differential migration between sexes, with more females stopping-over at the mouth of the Vistula River than elsewhere in western Europe. In the western Palearctic, females might follow more eastern routes than males, heading directly to wintering areas of tropical and subtropical Africa where they outnumber males (Cramp & Simmons 1983). The presence of longer-winged birds in the second wave of adult passage and the almost complete absence of birds in primary moult among late migrants suggest that these birds are probably mostly females originating from a different population.

Despite our data showing that some birds migrate in active primary moult, only moult stages close to suspension were actually observed, suggesting that primaries were shed before the beginning of the journey and apparently confirming that, like most waders migrating with long non-stop flights, Grey Plovers tend to maintain a temporal segregation between migration and moult.

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Selostus: **Aikuisten ja nuorten tundrakurmitsoiden syysmuutto Vistula-joen suulla Puolassa**

Kirjoittajat rengastivat yhteensä 130 nuorta (1-kv) ja 65 aikuista (+1-kv) tundrakurmitsaa heinä-lokakuussa vuosina 1983–1996 Vistula-joen suulla Puolassa. Kirjoittajat havaitsivat aiemmin laskenta-aineistoissa todetun ilmiön, että aikuiset tundrakurmitsat muuttavat huomattavasti nuoria lintuja aikaisemmin. Aikuisten muuton ajoittuminen oli kaksihuippuista suurimpien yksilömäärien sattuessa toisaalta elokuun puoliväliin ja toisaalta elosyyskuun vaihteeseen. Nuorten lintujen syysmuuton mediaani oli syyskuun lopussa (Kuva 1). Aikuislintujen siiven, pään ja nokan pituusmitat olivat keskimäärin suurempia kuin nuorilla yksilöillä mutta jalkojen mitoissa ei havaittu eroa ikäluokkien välillä (Taulukko 1). Aikuisten yksilöiden ruumiin massa pysyi vakaana koko muuttoperiodin ajan mutta nuorilla linnuilla havaittiin selkeä massan lisääntyminen kohti muuttokauden loppua lokakuussa (Kuva 3). Aikuiset linnut (174 g) olivatkin keskimäärin 6 g nuoria lintuja (168 g) painavampia, jos ei oteta lukuun lokakuussa pyydystettyjä nuoria lintuja (206 g). Aikuislintujen joukossa aikaisemmin (ennen 23. elokuuta) muuttaneet yksilöt olivat lyhyempisiipisiä kuin myöhemmin muuttaneet. Vain muutaman aikuislinnun havaittiin sulkivan käsisulkiaan muuton aikana (Taulukko 2).

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