MOULT, MASS AND MIGRATION OF GREY PLOVERS *PLUVIALIS SQUATAROLA* WINTERING IN SOUTH AFRICA

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Data on 355 Grey Plovers *Pluvialis squatarola* trapped in South Africa in 1971-1997 were used to describe seasonal body mass variation and moult in relation to their very long migrations. The estimated duration of adult primary moult, 131 days, was similar to that observed in India and 30-40 days shorter than durations reported for localities in Europe. All birds in their first and second year of life oversummering in South Africa underwent a complete moult between their first boreal spring and second boreal summer. The presence of two concurrent or consecutive primary moult cycles was observed in 35% of second-year birds. It is suggested that the primary moult of first or second-year birds might be considered as an anticipated post-breeding moult rather than a postponement of the post-juvenile body moult or a delayed pre-migratory one. If this hypothesis is confirmed, the second primary moult cycle observed in oversummering first-year Grey Plovers would be a supplemental post-breeding moult. This cycle may have no adaptive value, occurring through the absence of endogenous cues which stop the moult. Migratory mass gain was observed only in birds which had completed or suspended primary moult. Departure mass (> 310 g) was reached by some individuals as early as 15 March, but most birds departed between 15-30 April. Grey Plovers left South Africa before having moulted into a complete breeding plumage.

Key words: *Pluvialis squatarola* - wing moult - plumage - annual cycle - fattening - migration

INTRODUCTION

To shed light on various aspects of the ecology of migrant waders, seasonal body mass variation has been widely studied in relation to migration and moult of contour and flight feathers (e.g. Pearson 1981, 1987; Johnson *et al.* 1989; Summers *et al.* 1989; Zwarts *et al.* 1990; Marks 1993; Pietsma & Jukema 1993). Data collected at the extreme limits of a species' geographical distribution are of great heuristic value because such areas wholly, or predominantly, host single populations and therefore present simplified situations (Thomas & Dartnall 1971; Tree 1977, 1979; Elliott *et al.* 1976; Waltner & Sinclair 1981; Summers *et al.* 1987a, 1989; Summers & Waltner 1989; Balachandran *et al.* in press). In the Afro-Palearctic migratory system, 20 species of Palearctic waders, including the Grey Plover *Pluvialis squatarola*, have their southern distributional limit in South Africa (Harrison *et al.* 1997). Grey Plovers breed in the High Arctic and perform biannual migration journeys between summer and winter ranges, covering long distances by non-stop flights. South Africa has a population of ca. 8800 Grey Plovers, occurring mainly along the Atlantic coast (Summers *et al.* 1987b; Underhill 1997). This paper describes seasonal body mass variation, moult and migra-
tion movements of South African Grey Plovers through the analysis of biometrics, moult and plumage data. These results provide a framework for discussing the moult and migration strategies adopted by this species and other waders wintering at subtropical latitudes.

STUDY AREA AND METHODS

Data from 355 Grey Plovers caught in South Africa in 1971-1997 were analysed. Of all birds 75% were trapped at Langebaan Lagoon (33°12'S, 18°07'E) and 16% at the Swartkops River estuary (33°45'S, 25°38'E); other sites each accounted for 0.1-3.4%. Grey Plovers were trapped mainly in mist-nets at or close to high-tide roosts; only a minority was caught by cannon-nets or dazzling. Birds were aged according to plumage characters (Prater et al. 1979; Cramp & Simmons 1983) and divided into the following categories: first-year birds (birds in their first year of life, from their arrival in juvenile plumage in October-November to 30 June), second-year birds (birds in their second year, from 1 July to the completion of their first primary moult in October-November) and adults (birds older than first-year birds, from arrival from breeding grounds in August to departure in April). Second-year birds were always excluded from adult category when identified, but ageing was problematic towards the end of the first primary moult, when juvenile feathers retained from the post-juvenile partial moult (some tertials, scapulars, rump and wing coverts) were lost. However, by comparing the more advanced stage of the moult of juvenile primaries with the timing of adult moult and the presence of juvenile primaries (more pointed, faded and abraded than adult primaries), the number of unaged birds was greatly reduced.

Body mass was recorded to the nearest gram with spring balances. No correction indices for body mass loss could be applied because the interval between capture and weighing the birds was seldom registered, although the period was generally less than one hour. Primaries were numbered from innermost (P1) to outermost (P10). Primary moult scores were recorded (Ginn & Melville 1983) and converted to percentage feather mass grown (Underhill & Joubert 1995). Moult parameters were estimated using the statistical method of Underhill & Zucchini (1988). This method considers three types of data, in relation to different scenarios of bird presence in the study area and sampling techniques, later supplemented with two more data types (Underhill et al. 1990). Our data fulfil the conditions of type 2 because adult Grey Plovers arrive in South Africa with the full set of old primaries, moult and then stay till pre-breeding migration. Some second-year birds showed two concurrent cycles of primary moult. In such birds, moult parameters were estimated separately for each of the two moult cycles. We assumed that moult speed and pattern did not differ between birds with one or two cycles.

The presence of breeding plumage was recorded in the field on a scale of 0 (full winter plumage) to 8 (full breeding plumage), or as a percentage of full breeding plumage. In the analysis, due to the small number of birds checked for plumage and different scales adopted, the following categories of percentage of breeding plumage were used: 0 = 0%, 1 = 1-28%, 2 = 29-56%, 3 = 57-84%, 4 = 85-100%.

Except where stated, seasons refer to the northern hemisphere. In some cases, dates were converted to days and numbered from 1 July to 30 June. Because the cycles of many biological events, such as moult of juvenile primaries or body mass variations, crossed the year limit set at 30 June, dates in the second year are given as additives.

RESULTS

Moult of primaries and contour feathers

No adult birds with active or suspended primary moult were observed on arrival in South Africa, suggesting that primary moult usually started in September-October after they had settled (Fig. 1a). The estimated duration (± SD) for adult
primary moult was $131 \pm 6\text{ d}$, from 30 September ($\pm 6\text{ d}$) to 8 February ($\pm 4\text{ d}$). The parameter of the variance in moult duration (the ‘standard deviation parameter’ of Underhill & Zucchini 1988) was estimated at $28 \pm 2\text{ d}$. Three adults were found in suspended primary moult, one in February and two in April, all with the outermost primary retained. The same pattern, but with the outer two primaries from the previous generation, was observed on a bird caught in November.

In first-year birds, the first observation of primary moult was on 10 January and the last one on 4 November of the second year (Fig. 1b). The estimated duration of primary moult was 194 days ($\pm 9\text{ d}$), from 19 April ($\pm 7\text{ d}$) to 20 October ($\pm 6\text{ d}$). The estimate of the standard deviation parameter was $36 \pm 6\text{ d}$. Twenty-four second-year birds (35%) showed two cycles of primary moult, and in 16 (24%) these were simultaneously active. In birds observed with two active moult cycles, the first cycle had always reached the same stage (P10 was growing), but the second cycle ranged from P2 to P9 (mean $\pm SD = 4.6 \pm 1.4$). Timing of the second cycle overlapped adult primary moult (Fig. 1c).

In September, less than 10% of adults were still in full breeding plumage, and most birds showed transitional plumage stages (Fig. 2).
From October, birds completed body moult and attained a full non-breeding plumage. From February, soon after they had completed primary moult, adults started to moult into breeding plumage. No birds were seen in full breeding plumage in April, the latest period of their stay in South Africa (Underhill 1997). Of 12 first-year birds examined in March-June, none had any breeding plumage feathers, and of 18 second-year birds examined in July-October, three (17%) showed traces of breeding plumage. Among the latter, one bird caught on 19 September had 45% of breeding plumage and had just started moult of juvenile primaries (primary score: 1110000000).

**Seasonal phenology of body mass**

From October to April, adults in active primary moult averaged 214 g. Body mass did not vary among these months (one-way ANOVA, $F_{6,76} = 0.44$, n.s.). However, in January and February, birds which had finished primary moult were heavier than birds in moult, and averaged ($\pm$ SD) 233 ± 16 g ($n = 6$) and 229 ± 39 g ($n = 11$), respectively. Evidence of a migratory body mass increase was observed in March (average 260 ± 33 g, $n = 49$) and April (average 301 ± 24 g, $n = 60$; Fig. 3). Assuming that the average mass of moult-}

![Fig. 3](image_url)  
**Fig. 3.** Seasonal distribution of body mass values for adults. The lines represent Lowess-regressions fitted to 50% of the points.

ing birds represents the initial mass, and that the average mass of the upper half of the frequency distribution of birds caught during the fattening period (March-April), 310 g, represents minimal departure mass (Zwarts et al. 1990), body mass increased approximately 45% (96 g). Birds that reached the threshold of 310 g, and were thus ready to start migration, were regularly found from 15 March to 30 April (Fig. 4). Their proportion was around 20% between 15 March and 15 April, suggesting that the number of newly moulted birds, ready to prepare for migration, equalled that of birds which had reached migratory values and had left. The significant increase in the proportion of birds ready to take off in the last 15 days of April (60%) suggested that the recruitment of birds for migration was completed.

Considering the strong relationship between the end of primary moult and the onset of migratory fattening (Fig. 3), and the observation that about 95% of the adult population had finished primary moult by 4 April (Fig. 1a), we assumed this date as the latest one on which birds started to gain body mass. These late birds had no more

![Fig. 4](image_url)  
**Fig. 4.** Frequency distribution of adults ready to take off (light shading) and still gaining mass (dark shading) against time. The first birds which reached the take-off threshold of 310 g appeared in February, but they were regularly present only after 16 March. After mid-April they outnumbered birds still gaining mass.
significantly between categories of the percentage of attained breeding plumage (one-way ANOVA, $F_{3,66} = 0.55$, n.s.).

First-year birds weighed less than adults upon their arrival in September-December, averaging 184 g vs. 216 g of adults ($t$-test = 4.6, $df = 71, P < 0.001$). Their body mass increased slowly throughout the winter, maintaining lower values than adults until May (Fig. 5a). Between January and March, the distribution of body masses was positively skewed (median = 204 g, mean = 213 g, SD = 28.7, skewness = 0.77, SE of skewness = 0.38, $n = 38$). Twenty-five percent of the first-year birds were heavier than 230 g (mean value of non-moulting adults in that period), suggesting that some first-year birds put on energy stores during the austral summer (Fig. 5b). However, none of them reached departure values. Second-year birds averaged ($\pm$ SD) 211.5 $\pm$ 13.0 g (range 183-244, $n = 56$) and did not show significant variation from July to December (ANOVA, $F_{4,51} = 0.599$, n.s.).

**DISCUSSION**

The onset of primary moult during the last phases of the breeding season has been reported from various sectors along the species’ Palearctic range and it probably involves mainly males (Hötker 1995; Gromadzka & Serra 1998). The proportion of birds showing signs of this early start of the moult varies at different stopover sites or wintering areas. At the Wash, England, 25-40% of adults had replaced from one to three primaries upon arrival in August (Branson & Minton 1976), and 11% had done so in the southern Baltic (Gromadzka & Serra 1998). Grey Plovers in South Africa did not present any indication of such suspension, as also recorded in Italy and India (Serra & Rusticali 1998; Balachandran et al. in press). The absence of such observations at sites where mainly wintering birds are present might be due to the prompt resumption of moult once they have settled. The low proportion of birds caught with the full set of old primaries - at all the sites men-
tioned above - might support this hypothesis. However, as the sex-ratio is probably not balanced in winter quarters, with females outnum­bering males in the southern part (Cramp & Sim­mons 1983), the higher proportion of females at the southern edge of Africa could contribute to explain this pattern.

On the winter quarters, moult duration varies from 90-100 days in England (Branson & Minton 1976), Dutch Wadden Sea (Boere 1976) and Italy (Serra & Rusticali 1998) to 127-131 days in India (Balachandran et al. in press) and South Africa. The existence of a distributional limit at ca. 20°N latitude, which possibly separates populations forced by local conditions to moult at maximum speed from others which are not constrained by the onset of a cold winter season and can therefore moult at an optimal speed for producing high-quality flight feathers, has been suggested to explain the presence of this geographical pattern of moult durations (Serra 1999). Adult Grey Plo­vers encounter benign conditions in South Africa. This allows them to moult during their whole period of presence, apart from the 3-4 weeks which precede departure. Despite the long season available for moulting, a small fraction of South African birds did not complete primary moult before migration, in contrast with India, where all adults moved northward with a full set of new primaries. However, the onset of moult in India is estimated as 1 September (Balachandran et al. in press), about 30 days earlier than in South Africa. The longer time required by Grey Plovers to reach South Africa may restrict the available period for moulting; birds that settle late in the season may not be able to complete moult before departure date. Grey Plovers wintering at the two latitudinal extremes of their Afro-Palearctic range may have developed a similar strategy in order to solve time constraints of different kinds.

Apparently, all first/second-year birds spending the boreal summer in South Africa moult their primaries between their first spring and second summer, implying that they do not return to the breeding grounds in that season. Primary moult of oversummering Grey Plovers has not been stud­ied in detail elsewhere. Available data suggest that the start of moult is probably deferred until May-June in the Mediterranean and northwestern Europe, and moult completion is likely to occur in August-September (Branson & Minton 1976; Pro­kosch 1988; Serra & Rusticali 1998). This different­ent moult timing could be linked to the longer period of presence of adults and more severe winter conditions at northern latitudes. Resource availability and competition with adults have been in­voked as factors affecting moult timing in first­year American and Pacific Golden Plovers Plu­vaisalis dominicus and Pluvialis fulva (Johnson 1985b, Sanderling Calidris alba (Myers et al. 1985) and Bristle-thighed Curlew Numenius tahitiensis (Marks 1993). As a rule, first-year birds settled on wintering sites some weeks later than adults and could have difficulty in maintaining an optimal energy budget in an environment not previously visited and already occupied by adults (Johnson 1985b). This scenario is appropriate for Grey Plovers because differential timing of settlement, lower body masses in first-year birds and intra-specific competition have been found at South African estuaries (Turpie & Hockey 1996), and also at the northern limit of the winter range (Johnson 1985a; Townshend 1985). This suggests that inexperienced first-year Grey Plovers have limited access to food resources, and can only moult primaries when adults are absent. This does not explain why there is not complete segregation between their first primary moult and adult presence, given that there are no time constraints for moult­ing in South Africa. First-year birds in South Africa started moult­ing when adults were gaining mass, i.e. when competition for resources should have been at its maximum. The same situ­ation seems to happen in Europe (Prokosch 1988).

If the lack of a 'pre-migratory' primary moult cannot be considered per se as a factor precluding northward migration in first-year birds (Johnson 1985b), it is nevertheless evident that the norm for Palearctic waders which winter in subtropical Af­rica and migrate in their first year is to undergo a complete moult of primaries or to change the outermost ones (Pearson 1974, 1977, 1981, 1984; Tree
1974, 1977; Elliott et al. 1976; Dean 1977; Prater 1981; Waltner & Sinclair 1981). It seems therefore that for waders travelling long distances, there is a direct relation between an early moult of primaries and migration, or, conversely, between late moult and oversummering. Chu (1994) proposed that retention of juvenile primaries in the first year was a primitive character of the wader ancestor. If this is the case, then a selective pressure should operate on arctic wader population wintering in the southern hemisphere, driving species which breed in their first year to perform a partial or complete pre-migratory primary moult (supplemental moult sensu Prater 1981) during their first winter, in order to migrate with new primaries.

If the advantage of moulting when intraspecific competition is at a minimum appears rather obvious for birds which are not compelled to migrate by breeding, the relationship between the moult of juvenile primaries and the second, often concurrent cycle of primary moult, which replaces feathers which have just finished growing, remains obscure. Perhaps, during the austral winter Grey Plovers - and other arctic waders - do not face ecological conditions severe enough to inhibit the start of the second cycle, as suggested for the Bristle-thighed Curlew in the Hawaii (Marks 1993).

As in other long-distance migrants, the seasonal timing of migration, breeding and moult of Grey Plovers are likely to be subject to endogenous control and strictly linked to each other (Berthold 1985, 1996). First-year birds that do not attain full breeding plumage, and do not migrate and breed, might not encounter physiological barriers to moulting. Low levels of sex-steroid hormones may be important in the lack of inhibition of the post-breeding moult (Hahn et al. 1992). If return to the breeding grounds and no primary moult in the first year of life were the ancestral conditions for waders (Chu 1994), the juvenile primary moult of oversummering Grey Plovers should be considered as an anticipated first post-breeding moult rather than a delayed phase of the post-juvenile moult. This hypothesis is supported by (a) the post-juvenile body moult ending before the onset of the juvenile primary moult (4-5 months before in Europe and North America), and (b) a small proportion of first/second-year Grey Plovers attain breeding plumage and delay juvenile primary moult to adult timing (Paulson 1995). Following this line of reasoning, the second primary moult cycle in oversummering birds might be considered as a supplemental post-breeding moult that proceeds until the switching on of endogenous cues, triggered by signals like the onset of unfavourable conditions or migratory fattening, stop the moult (Hahn et al. 1992; Berthold 1996). This second cycle may therefore have no adaptive value.

Migratory fattening was observed in adults which had completed or suspended primary moult, while adults in active moult and most first-year birds did not gain mass. Our estimate of an 'individual' daily increase rate of 1.7% falls close the range of 1.0-1.5% calculated for populations of other waders preparing for migration in South Africa (Middlemiss 1961; Elliott et al. 1976; Summers et al. 1987a, 1989; Summers & Waltner 1979) and to the 1.8% observed in Grey Plovers wintering in Britain (Branson & Minton 1976). These rates are much lower than the average daily mass increase of 3.5% at the German Wadden Sea in spring (Prokosch 1988) and from the maximum theoretical rates of c. 4.5% for waders (Zwarts et al. 1990). Zwarts et al. (1990) pointed out that fattening rates of waders at wintering sites may be underestimated, because mean mass is biased downwards by prolonged departure periods and variable increase rates. There are also two possible biological reasons why waders do not gain mass at the maximum rate of metabolizable energy intake (Zwarts et al. 1990): (a) the advantage of carrying extra fat loads for the shortest possible period does not balance the risk of missing the body mass departure value at the latest possible departure date; (b) food conditions are poor and do not allow mass gain at the maximum metabolic rate. However, there are indications that food conditions play only a minor role as short-term factors, because birds are able - to some ex-
tent - to compensate for food reductions by increasing foraging activity, and inter-annual variations in food supply are not correlated with changes in the increase rates (Zwarts et al. 1990; Biebach 1996). Average feeding conditions seem therefore to act in the longer term, on the evolution of increase rates at a population level (Zwarts et al. 1990).

Departure values of body mass were observed not only in birds at the final stages of pre-breeding body moult, but also in birds at initial stages of body moult or before it. Grey Plovers seem therefore to leave South Africa before completing moult into a breeding plumage, showing as wide a range of plumages at departure as in Guinea-Bissau (Ruiters & Fokker 1998) and Venezuela (McNeil 1970). That waders in full breeding plumage have greater body masses than birds at earlier stages has been described for various species and at different wintering areas (Johnson 1985b; Pearson 1987; Zwarts et al. 1990; Morrison & Harrington 1992). It appears that at sites nearer breeding grounds, where the onset of migration can be delayed, higher proportions of waders complete the pre-breeding body moult. In South Africa, the scheduling of post-breeding moult and departure does not always allow pre-breeding body moult to be completed. In this case, the urge of moving northward seems to be stronger than that of attaining a full breeding plumage.

Although some adults appeared ready to leave for northward migration from 15 March, but most departures were between 15-30 April. This timing is consistent with census data from three of the most important South African wetlands, where numbers decreased abruptly between April and May (Taylor 1956; Liversidge et al. 1958; Pringle & Cooper 1975; Martin & Baird 1987; Spearpoint et al. 1988; Velasquez et al. 1991). A small proportion of first-year birds gained mass between January and March, implying preparation for migration, although first breeding attempts in Siberia are thought not to occur before an age of 2-3 years (Cramp & Simmons 1983). However, fat first-year birds were observed on northward migration in North America, and specimens from American breeding grounds were aged as first-year birds, establishing that breeding may take place at this age (Paulson 1995). Carrying extra fat loads is costly and therefore avoided if not strictly necessary (Houston & McNamara 1993; Gosler et al. 1995; Pilastro et al. 1995). First-year body mass gain occurred earlier in the season than in adults and adult departure body mass values were not reached, but ca. 25% of first-year birds prepared for an energy demanding event. They could use these stores either to migrate towards sites which offer better conditions for moult - such as Langebaan Lagoon, Berg River or Swartkops estuaries and adapt to the new environment, or embark on longer, transcontinental journeys. There is evidence for both movements: a colour-ringed first-year bird, marked at Port Alfred, Eastern Cape, on 29 March 1992 was observed 121 km west at Swartkops estuary on 13 July 1992 (A.J.T. pers. obs.) and a first-year ringed at Walvis Bay, Namibia, in March 1975 was recovered the following August in Crimea, Ukraine (Underhill 1997). In northern Europe, a small and highly variable proportion of first-year Grey Plovers oversummer, suggesting that a return to the breeding quarters when the birds are one year old occurs regularly (Boere 1976; Prokosch 1988; Summers et al. 1997). In South Africa, more than 10,000 km further away from the breeding grounds, most birds remain until two years old. Yet, some first-year Grey Plovers may nevertheless initiate northward migration.

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SAMENVATTING

Op basis van de gegevens over rui en lichaamsgewicht van 355 Zilverplevieren *Pluvialis squatarola* die in de periode 1971-1997 in Zuid-Afrika zijn gevangen, werden de seizoensgebonden veranderingen in gewicht en in de rui van lichaamsveren en slagpennen beschreven en geïnterpreteerd in het licht van het trekgedrag van de soort. De gemiddelde tijd die nodig was om de slagpennen te ruien, werd geschat op 131 dagen. Deze schatting komt overeen met die voor Zilverplevieren die in India ruien, maar is 30-40 dagen korter dan de schatting voor Zilverplevieren die in Europa ruien. Alle eerstejaars vogels ondergingen aan het einde van hun eerste levensjaar een complete rui van lichaamsveren en slagpennen. Dit gebeurde een paar maanden eerder dan bij volwassen vogels die naar de broedgebieden waren ge­weest. Een deel van de jonge vogels vertoont na de (noordelijke) zomer opnieuw een slagpenrui in dezelfde tijd dat de volwassen vogels ruiden. De laatste rui van de jonge vogels wordt geïnterpreteerd als een *toegevoegde* rui. Deze rui heeft geen duidelijke functie, maar zou een een expressie kunnen zijn van endogene processen kenmerkend voor volwassen Zilverplevier­ren. Overigens begonnen Zilverplevierren pas met opvetten voor de trek naar het noorden nadat deze waren gestopt met hun slagpenrui; soms werd de slagpenrui onderbroken. Lichaamsgewichten die kenmerkend waren voor wegtrekkende vogels (>310 g) werden vanaf 15 maart bereikt, hoewel de meeste individuen pas tussen 15 en 30 april vertrokken. Alleen volwassen Zilverplevierren vertrekken uit Zuid-Afrika naar de broedgebieden. Bij vertrek hebben ze over het algemeen nog geen compleet broedkleed.

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