Breeding origins of wader populations utilizing the Dutch Wadden Sea, as deduced from body dimensions, body mass, and primary moult
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Figure 20: The distribution in percentages of 4 stages of primary moult for the twelve species and three locations in the Wadden Sea. The data span the period between July and December. For each species and location the number of birds captured is presented just above the X-axis. The four stages of primary moult are from bottom to top: old, actively mouling, suspended moult and completed.
Many of the Ringed Plovers, Curlew Sandpipers, and Greenshanks captured did not moult their primaries in the Wadden Sea (Fig. 20). For all other species moult was observed rather often. Most waders returning from the breeding grounds started their primary moult during August (Fig. 21). Eurasian Curlews were an exception with an estimated mean starting date of 22 July. The estimated mean starting dates of Dunlin and Redshank were respectively 4 and 7 August. Sanderling and Ruddy Turnstone started around 20 August with Red Knot following 8 days later. Bar-tailed Godwit and Grey Plover were the only species, which started as late as early September. Dunlins and Red Knots needed 53-57 days for their primary moult, while Grey Plovers and Eurasian Curlews needed 80-90 days. Occasionally a bird was caught in an advanced stage of primary moult during June, July or August. These birds often had a very worn plumage with remnant characters of first winter or juvenile plumage (Boere 1976) and were considered as summering birds (second summer- & non-breeding birds), which had started their primary moult already in June, a few weeks after the mass departures of the arctic migrants from the Wadden Sea to their breeding grounds. The year-to-year variation in start of primary moult was estimated to range between 20 (Dunlin, Red Knot) and 30 days (Grey Plover, Eurasian Curlew).

Figure 21: Estimates of the mean start and duration of primary moult in the wader species studied. The thick lines present the mean start and duration. The thin lines present the 95% confidence intervals of the estimates. A. (black lines) birds returning from their breeding grounds, and B. (grey lines) summering birds (non-breeders, immatures) in an advanced stage of primary moult.
There is a large degree of spatial differentiation with respect to occurrence of primary moult (Fig. 20). For instance, the Red Knots and Bar-tailed Godwits on Vlieland and Schiermonnikoog are often moultig, while they nearly never moult along the mainland coast. The moult-data of Grey Plovers, Dunlins, and Ruddy Turnstones show the same pattern but less pronounced.

Redshank seems to be the exception with less moulting individuals on Schiermonnikoog as compared with both other sites. Since temporal variation might cause these differences, the data of July and August were analysed in a bit more detail (Fig. 22). The staging populations of Grey Plover, Red Knot, and Bar-tailed Godwit along the Frisian coast included the highest percentages non-moulters, while they were lowest on Schiermonnikoog. There were also significant differences, once the birds had started primary moult. One bird might start its primary moult intensely with many feathers being shed simultaneously, while another seems to restrict its gap size. Relatively many Redshank and Greenshank tended to have large gaps on Vlieland in comparison to Schiermonnikoog, or additionally relatively many Knot, Dunlin, Bar-tailed Godwit, Eurasian Curlew, and Greenshank tended to have small gaps on Schiermonnikoog. However, this was not tested statistically. Relatively many birds with small gaps were present along the Frisian coast (Dunlin and Redshank) and Schiermonnikoog

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**Table 17. Results of GLM-analysis relating the number of simultaneously moulted primaries to the number of new primaries already grown and to the catching site. Significance levels: * 0.01 < P < 0.05; ** 0.001 < P < 0.01; *** P < 0.001.**

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<tr>
<th>Species</th>
<th>df</th>
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<th>F</th>
<th>R²</th>
<th>sign. F</th>
<th>sign. F</th>
<th>Intercept</th>
<th>N of new primaries</th>
<th>Vlieland</th>
<th>Frisian coast</th>
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Figure 22: The occurrence of primary moult in adult waders captured in the Wadden Sea during July and August. A distinction is made between non-moulters and moulters. In the moulters, a distinction is made between birds with 'small' or 'large' gaps in the wing. The definition of 'small' gaps is according to Holmgren et al. (1993b): 1 primary shed with raggedness score 3 or lower, 2 primaries shed with score 7 or lower, 3 primaries shed with score 8 or lower, 4 primaries shed with score 7 or lower, 5 primaries shed with score 6 or lower, 6 primaries shed with score 6 or lower, 7 primaries shed with score 7 or lower, 8 or 9 primaries shed with score 4 or lower.
(Eurasian Curlew and Greenshank). In a GLM-analysis the number of simultaneously moulted primaries were analysed in dependence of the number of new primaries already grown and the location (Table 17). Location appeared to be a significantly differentiating factor in 6 of the 12 species. Moulting Dunlin, Bar-tailed Godwits, and Eurasian Curlew have larger gaps on Vlieland than on Schiermonnikoog and moulting Ringed Plovers, Grey Plovers, Red Knots, Dunlin, and Redshank all had significantly smaller gaps along the Frisian coast than on Schiermonnikoog. In most of the species analysed, the Frisian coast populations were extreme because they had the highest proportions non-moulters and/or the smallest gaps in the wings and/or the lowest number of simultaneously growing feathers.

Waders nearly always suspend rather than arrest their moult (Cramp & Simmons 1983). Moulting suspender resume their primary moult: the new feathers continue to grow, but no new feathers are shed. They continue to moult later during that same non-breeding season under warmer circumstances. When they arrest moult, they skip a cycle with a set of new and old feathers and start again next year after the breeding season. Since moult suspension of waders in autumn mostly precedes migration further south, it is of interest to know when and where birds were suspending their moult. The Grey Plover, being the latest species starting

![Graph showing suspension rates of primary moult in five wader species during post breeding.](image)

*Figure 23: Suspension rates of primary moult in five wader species during post breeding.*
its primary moult, is the species with by far the highest percentages moult suspension (Fig. 23). The suspension percentage in this species is increasing to 60% of the adults captured in November. Redshank populations show a peak in suspension percentages during September. The mainland coast populations of Red Knot ($\chi^2 = 15.465; df \, 2; \, P < 0.000$), Dunlin ($\chi^2 = 12.594; df \, 2; \, P < 0.002$), and Redshank ($\chi^2 = 22.802; df \, 2; \, P < 0.000$) have the highest percentages of moult suspension amongst the three locations with resp. 5.3, 1.1, and 8.1%. The duration of primary moult is of influence on the quality of the primaries renewed (Serra 2001): growing more durable primaries -with higher concentrations of melanins- takes more time.

Summarizing, three species hardly ever moult their primaries in the Wadden Sea: Ringed Plovers, Curlew Sandpipers, and Greenshanks. The other species have a large degree of spatial variation with respect to the primary moult pattern. The inhibition of primary moult in the wader populations along the mainland coast is striking with hardly any mouling Red Knots and Bar-tailed Godwits and fewer mouling Grey Plovers, Dunlins, and Ruddy Turnstones. When birds were mouling their primaries, the Ringed Plovers, Grey Plovers, Red Knots, Dunlin, and Redshank along the Frisian coast had smaller gaps, since they shed fewer primaries simultaneously. Incidence of moult suspension was also highest along the mainland coast in Red Knot, Dunlin, and Redshank.

The Vlieland populations of Red Knot, Dunlin, Bar-tailed Godwit, Eurasian Curlew, Redshank, and Greenshank shed more primaries simultaneously or had larger gaps in the wings than their Schiermonnikoog-conspecifics. The Grey Plover had the highest suspension rate amongst the species studied. These differences in primary moult patterns might be caused by differences in migration strategies, time constraints (Serra 2000) or in population composition.

Some of the most pronounced results for species:

1. **Ringed Plover.** Our results agree with Haberer’s (1994) results showing low percentages of adult Ringed Plovers with actively mouling primaries in the Wadden Sea. On the other hand, 50-90% of the adult Ringed Plovers caught in the Wash undergo their primary moult in the area (Johnson 1985). Even though the primary moult percentages range between 1 and 86% in other British estuaries (Eades & Okill 1976, Clapham 1978, Insley & Young 1981), they are nearly always higher than the ones in the Wadden Sea.

2. **Grey Plover.** About 10% of the Grey Plovers, captured soon after arrival in August (adults with low energy reserves, n = 231), had suspended primary moult prior to their departure
to the Wadden Sea. This percentage is similar to the 11% for the southern Baltic (Gromadzka & Serra 1998), smaller than the 18% in the Polish Puck Bay (Krupa & Krupa 2002) and the 25-40% for the Wash (Branson & Minton 1976) but higher than the 5% presented for the Wash (Serra et al. 2006). No moult suspension was detected amongst the recent arrivals at more southerly latitudes like NE-Italy (Serra & Rusticali 1998), SE-India (Balachandran et al. 2000), and S-Africa (Serra et al. 1999). The Nearctic breeding population starts its primary moult at the breeding grounds, whilst only few birds do so on the Palearctic breeding grounds (Prokosch et al. 1993, Engelmoer & Roselaar 1998, Exo & Stepanova 2000).

3. Dunlin. Nearly all adults started post-breeding moult immediately after arrival in the area or were mouling when arriving in the area. More than 30% of the Dunlin present on the Baltic staging grounds combine short stays with active primary moult (Gromadzka 1989, Holmgren et al. 1993a). These birds thus enter the Wadden Sea with growing primaries. The proportion of birds not in primary moult in the Wadden Sea immediately after the breeding season is accordingly small compared with other species in the area. Dunlins on the island sites also started their primary moult 2-3 weeks earlier than the ones captured along the Frisian coast.