Mass, moult, migration and subspecific status of Red Knots *Calidris canutus* on the Frisian Wadden Sea coast, The Netherlands

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Combining existing knowledge from the literature with data on biometrics, primary moult and recapture rates of Red Knots *Calidris canutus* along the Frisian Wadden Sea coast of The Netherlands, it is argued that in summer and autumn the following groups occur: (1) a small group of summering sub-adult *islandica*, which moult part of their primaries, then suspend moult and move for the winter to England or France where the moult is finished, (2) a small group of adult *islandica* which start primary moult and finish it elsewhere in the Dutch Wadden Sea and (3) large groups of adult and juvenile *canutus* which use the area to store fat for a southbound migration to W Africa.

INTRODUCTION

Dick et al. (1976) were the first to show that, in the nonbreeding areas of Europe and Africa, two populations of Red Knots can be distinguished on the basis of biometrics. They demonstrated that a shorter-billed population from Greenland and NE Canada winters in Europe and that a longerbilled population from Siberia migrates through Europe en route to and from winter quarters in W Africa. Roselaar (1983) recognized the two populations as subspecies named respectively islandica and canutus. Material from Siberia was however lacking. Later, many ornithologists (e.g. Nehls 1987, Prokosch 1988, Gromadzka 1992, Meissner 1992, Schekkerman et al. 1992) tried to separate their Knots caught for ringing into the subspecies *canutus* and *islandica*, based on Dick et al. (1976) and Roselaar (1983). Tomkovich & Soloviev (1996) measured live birds from Siberian breeding areas and found that the measurements of Knots from the Taimyr Peninsula (the breeding area closest to Europe) closely agree with those of supposed migrant canutus in spring and autumn in W Europe.

From 1973, the Wader Working Group Friesland (later part of the Fryske Feriening foar Fjildbiology (FFF)) has counted waders along the mainland coast of the Wadden Sea in the province of Friesland, The Netherlands. Since 1980, the Wader Ringing Group of the FFF has been ringing waders on the Frisian coast near Holwerd (53°23'N, 05°55'E, Fig. 1). In this paper, counts and ringing data are analysed to contribute to our knowledge of the Knots that occur on the Frisian Wadden Sea coast.

METHODS

From 1973 to 1991, 91 high-tide counts were made on the Frisian coast, of which 83 included the section east from the pier of Holwerd for a distance of 2.5 km (Holwerd East). Between 2 August 1992 and 10 February 1996, the waders in this section were on average counted fortnightly, with a total



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of 78 counts altogether. The number of counts per month varied from four in March to nine in August and September.

Between 1980 and 1995, 326 Knots were caught in mistnets during nocturnal high tides. For each bird, wing length (maximum length of flattened and straightened wing to the nearest mm (Svensson 1984)), bill length (the length of the exposed culmen to the nearest 0.1 mm), body mass (to the nearest gram) and primary moult were recorded. Primary moult was scored according to the method of Ashmole (1962) in which old primaries have a score of 0, new ones 5, and the growing feathers scores of 1–4. Primaries are numbered from inside to outside from 1 to 10.

Three age-classes were separated: juveniles (born in the year of catching), sub-adults (born in the year before catching) and adults (born at least two years before catching) (Prater *et al.* 1977).

RESULTS

Counts

Knots can occur at all times of year on the Frisian mainland coast, but they are often absent, especially in the east. The maximum ever recorded was 7,650, but most counts are of <3,000. On the Holwerd East section (the ringing area), >25 birds were recorded on 16 out of 83 counts during 1973–1991, especially in May (5/13 counts), August (3/4) and September (3/11). The highest number was 760 on 29 October 1988, though on most days when Knots were present there were no more than a few hundred. In winter, they were generally absent. In 1988, Knots were recorded in all counts from May to October.

During 1992–1996, >25 Knots were recorded at Holwerd East during only 12 of the 78 fortnightly counts, but between 24 July and 16 August they were present most of the time (Fig. 2). Outside this period, large numbers were present on only four days: 5 March, 6 May and 26 November 1995 and 5 June 1993.



Fig. 1. Location map showing the Frisian mainland coast of the Dutch Wadden Sea, the study area and other places mentioned in the text.

Ringing

During March-May 1980–1995, only three Knots were caught at Holwerd East during 36 nights. Between 15 July and 10 November of these years, however, 323 Knots were caught in 73 nights. This analysis relates to these 323 birds.

Before 1988, only a few Knots were caught, but subsequently they were caught with more regularity. From 21 July to 31 August, most were adults; later most were juveniles (Fig. 3). Wing and bill lengths of the adults decreased significantly from late July to the end of August (Equations 1 & 2, Table 1). Wing lengths and bill lengths of the juveniles were significantly shorter than those of the adults, with differences of 6.7 mm and 1.2 mm on average respectively (Table 1; wing, p<0.001, t = 13.55, d.f. = 316; bill, p<0.001, t = 5.35, d.f. = 316). The five sub-adults had significantly shorter wings and bills than the adults (Table 1; wing, p<0.001, t = 5.91, d.f. = 208; bill, p<0.05, t = 2.09, d.f. = 208). They also had significantly shorter wings than the juveniles (p<0.01, t = 2.71, d.f. = 116),



Fig. 2. Counts of Red Knots at Holwerd East between 2 August 1992 and 10 February 1996, plotted in 10-day periods (decades).

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Table 1. Wing and bill length of Red Knots caught at Holwerd.

Time period		Wi	ng	Bill		
	n	mean	SD	mean	SD	
Adults						
21-30 July	37	171.9	3.77	34.60	1.78	
1-10 August	85	171.1	4.03	34.60	1.93	
11-20 August	72	170.3	4.72	34.03	1.69	
21-31 August	8	168.1	2.75	33.66	2.07	
SeptOct.	3	166.7	6.66	33.10	2.93	
Total adults	205	170.8	4.31	34.34	1.85	
Sub-adults						
All dates	5	159.2	5.40	32.58	2.09	
Juveniles						
All dates	113	164.1	3.94	33.15	1.97	

but their bill lengths were not significantly different (t = 0.63, d.f. = 116).

- Equation 1: Wing = $174(\pm 1) 0.0800(\pm 0.0314)$ (Date) where Date is days from 30 June; p<0.05, R-Sq = 3.1%
- Equation 2: Bill = $35.9(\pm 0.5) 0.0387(\pm 0.0134)$ (Date) where Date is days from 30 June; p<0.01, R-Sq = 3.9%

In August, adults are heavier than juveniles (Fig. 4). The mean weights of adults fluctuate, but those of juveniles increase steadily from mid-October. Plots of the frequency distribution of adult weights for the third 10-day period of July and the first and second 10-day periods of August (Fig. 5) show that heavy birds are caught in each period, though the proportion increases from one to the next.

Thirteen birds were in primary moult: eight adults with low scores (2–15) and five sub-adults with higher scores (30– 35). One bird with a moult score of 35 had suspended moult and another bird with a score of 34 appeared to be about to suspend (because the 7th primary was almost fully grown and the 8th had still not dropped). A bird caught in mid-October had completed its primary moult and there was no criterion for determining whether it was an adult or sub-adult.

The measurements of adults, with and without primary moult, were similar (Table 2; wing, t = 0.12, d.f. = 202; bill, t = 1.22, d.f. = 202), but as mentioned above the sub-adults, all of which had high moult scores, were smaller than the adults. The average weights of the five sub-adults were lower than those of the adults (though not significantly so, t = 1.45, d.f. = 208), despite the fact they included two heavy birds with suspended/almost suspended moult and body masses of 170 and 181 g. The average weight of the other three subadults was only 133.7 g. They were all in active moult. The mid-October bird that had completed its moult is not included in Table 2. Its biometrics were: wing 161 mm, bill 35.4 mm, weight 151 g.

Ringing at Holwerd East resulted in six recoveries: Germany (3), Sweden (2) and France (1) (Table 3). All these birds were adults when caught at Holwerd and showed no primary moult. There was also one re-trap in September of a juvenile 10 days after ringing. During this period, its mass had increased from 122 to 133 g.

DISCUSSION

Knots occur regularly on the Frisian mainland coast. Since counts began in 1973, thousands have been recorded regularly, especially on the western sections at Westhoek and east of Zwarte Haan (Timmerman 1974, Engelmoer *et al.* 1983, Wader Working Group FFF unpubl. information). Further east, such as at Holwerd, a few hundred occasionally occur during spring or autumn. Before 1988, Knots were rarely caught at Holwerd East, but from then on, they were caught regularly.

Only in late July and early August do Knots occur in both the counts by day and the catches at night (Figs 2 & 3). During the rest of the year, they are lacking in most counts,



Fig. 3. Age composition of Red Knots caught at Holwerd in 10-day periods (decades).



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Fig. 4. Mean weight (± 1 s.d.) of adult and juvenile Red Knots caught at Holwerd plotted against date in 10-day periods (decades).

whereas they are caught regularly at night until November. This may be due to the use of different high-tide roosting sites by day and by night, as is the case in the Balgzand area in the western Wadden Sea (T. Piersma pers. comm.). The lack of Knots in the catches before 1988 could also reflect a shift in night-time roost sites. In spring, Knots have only rarely been seen by day or caught at night.

During 21 July to 20 August, practically all Knots at Holwerd are adults or sub-adults, though the proportion of sub-adults, which are already in advanced primary moult, is very low (Fig. 3). Some or possibly all of the sub-adults suspend primary moult to finish it elsewhere (Table 2). Their wing and bill lengths are exceptionally small (Table 1). Bill lengths of sub-adult Knots are normally equal to those of adults, but wing lengths are on average 7 mm shorter (Roselaar 1983). The sub-adults still had their juvenile outer primaries when caught and these were heavily abraded. However, even allowing this, it is likely that the wing lengths of the subadults were substantially shorter than those of the adults. The mean bill-length of an even mix of males and females would be 32.4 mm for *islandica* and 34.7 mm for *canutus* (Table 2, Engelmoer & Roselaar 1998). Therefore the bill-lengths of the sub-adults (mean 32.58 mm) agree best with those for *islandica* though the possibility that they include small *canutus* cannot be excluded. The measurements of the adults, especially the bill lengths, suggest *canutus* (Table 2, Engelmoer & Roselaar 1998).

Only a few of the adult Knots had started primary moult and these were still in the early stages. The fact that none were caught in more advanced moult shows that they leave



Fig. 5. Percent frequency distribution of the weights of adult Red Knots caught at Holwerd in three 10-day periods (decades).

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Primary moult	n	Wing		Bill		Body mass	
		mean	SD	mean	SD	mean	SD
Adults							
None	196	170.8	4.2	34.37	1.85	166.1	23.3
Moult score ≤ 15	8	171.0	6.2	33.55	2.07	158.5	28.1
Sub-adults							
Moult score ≥ 30	5	159.2	5.4	32.58	2.09	150.4	23.3
Biometrics of the sul	b-species accord	ling to Engelmoer	& Roselaar (19	98)			
islandica males	87	169.6	4.4	31.2	1.4		
islandica females	64	173.9	4.0	33.7	1.3		
canutus males	38	169.0	4.2	33.7	1.6		
canutus females	15	173.2	3.8	35.8	1.6		

Table 2. Biometrics of adult and sub-adult Red Knots caught at Holwerd compared with those for the sub-species *islandica* and *canutus* (from Engelmoer & Roselaar 1998).

Holwerd to carry out their main moult elsewhere. Suspended moult was not found among the adults. Therefore, assuming that they do not migrate in active moult, it is likely that they finish their moult elsewhere in the Wadden Sea. On the barrier islands of Schiermonnikoog and Vlieland, the majority of adult Knots caught in September are in advanced primary moult (Boere 1976), and this suggests that the Holwerd birds may possibly complete their moult there.

Most of the adults do not moult their primaries at Holwerd and the frequency distribution of their weights is indicative of fat storage (Fig. 5). As their measurements would suggest they are *canutus*, they probably continue migration and moult on their West African wintering grounds. Only one Knot, a juvenile, was re-trapped (10 days after ringing, Table 3). In contrast, data for Dunlin *Calidris alpina*, a species that moults its primaries on the Frisian coast, show that 1.5% (39/2,592) are re-trapped in the same or later years (Wader Working Group FFF unpubl. information). The difference in the recapture rate between Knots and Dunlins therefore supports the suggestion Knots visit the coast at Holwerd for only a short time before migrating further.

The wing lengths and bill lengths of adults caught decrease between late July and late August (Table 1). Probably early catches consist of more females, which are larger, and later ones more males. This arises because females leave the breeding areas before males, and the males care for the chicks (Cramp & Simmons 1983). Using the formula of Tomkovich & Soloviev (1996) to separate the sexes, the proportion of males caught increases from 49% in the last ten days of July to 68% in the middle ten days of August. Differences in timing of migration between males and females may also explain the plateau in the mean weights of adults during August (Fig. 4). At first in late July, females arrive and gain weight before migrating; later males with low body mass arrive and then also gain weight before departing.

On average the wing lengths of juvenile Knots are 7 mm shorter than in adults but bill lengths are similar to adults only 1–2 months after fledging (Roselaar 1983). Wing lengths of the juveniles caught at Holwerd were on average of 6.7 mm shorter than in the adults (Table 1). Bill lengths were only 1.1 mm shorter. Therefore it appears that the juveniles belong to the same population as the adults. The measurements of our juveniles are similar to *canutus* caught in Poland (Gromadzka 1992, Meissner 1992). However, the weights of the juveniles at Holwerd, especially in October, are much higher than in Poland. This may mean that juveniles at Holwerd are preparing to depart direct to W Africa.

Adults at Holwerd weighed on average 165.7 g and were

Table 3.	Ringing	recoveries	of Red	Knots	caught	at	Holwerd.
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Ring	Sex/age	Ringed (o), Recovered (+), Date and Place				
Arnhem	? adult	0	29 July 1980	Holwerd 53°23'N, 05°55'E		
K 571.379		+	19 March 1987	Schleswig-Holstein Germany 54°23'N, 08°38'E. Found freshly dead, lighthouse victim.		
Arnhem	F adult	0	2 August 1991	Holwerd		
K 860.318		+	27 July 1995	Öland Sweden 56°12'N, 16°24'E, controlled		
Arnhem	? adult	0	22 August 1992	Holwerd		
K 860.612		+	2 September 1993	Pas de Calais France 50°57'N, 01°50'E, shot		
Arnhem	? juvenile	0	12 September 1995	Holwerd		
K 939.601		+	22 September 1995	Holwerd, retrapped		
Helgoland	F adult	0	17 May 1981	Nordfriesische Inseln Germany 54°25'N, 08°48'E		
7.614.295		+	30 July 1992	Holwerd, controlled		
Helgoland	M adult	0	19 May 1987	Nordfriesische Inseln Germany		
7.696.105		+	5 August 1995	Holwerd, controlled		
Stockholm	? sub-adult	0	21 August 1988	Hålland Sweden 57°18'N, 11°54'E		
4.270.381		+	17 August 1991	Holwerd, controlled		

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much heavier than those in July and August in Poland (105 g: Gromadzka 1992, Meissner 1992) and in the Dutch Delta area (141 g: Schekkerman et al. 1992). It has been suggested that, in Poland, it is only fuel-depleted Knots that pause briefly to feed before continuing as soon as possible to major stopover sites in The Netherlands (Piersma et al. 1992). In the Delta area, most adults moult their primaries. In contrast, the Wadden Sea coast at Holwerd seems to be a stopover site, used mainly for storing fat before further migration. As the chance of catching stopover migrants in the short time between attaining maximum weight and departure is not great, it is likely that average departure weights of all birds are similar to the maximum weights recorded. Ten per cent weighed 200 g or more (Fig. 5) and this suggests that the birds would be capable of a direct non-stop flight to W Africa, the main wintering area of canutus (Piersma et al. 1992).

It is thought that most Knots first breed in their third calendar year. Sub-adults summer on the wintering grounds where they start moulting early, in advance of the adults (Cramp & Simmons 1983). Sub-adults at Holwerd should therefore belong to the *islandica* population that winters in W Europe and not to *canutus* that winters in W Africa. It would seem that the measurements confirm that this is the case. Very few sub-adults were recorded at Holwerd – only 2% that were not juveniles. This supports the suggestion that the Knots at Holwerd belong mainly to a population that does not winter in W Europe.

Based on current ideas (Davidson & Wilson 1992, Piersma *et al.* 1992, Tomkovich & Soloviev 1996, Engelmoer & Roselaar 1998), representatives of the following Knot populations occur at Holwerd in summer and autumn: (1) a small group of summering sub-adult *islandica*, which moult a proportion of their primaries, but subsequently suspend this moult and move to England (where 1% of Knots arrive with suspended moult (Anon 1981)) or France to finish moult and overwinter, (2) a small group of adult *islandica* which start primary moult, do not suspend, but move to continue moulting elsewhere in the Wadden Sea and (3) a large group of adult and juvenile *canutus* which use the area only to store fat (and not to moult) before migrating to W Africa.

In this paper, existing knowledge from the literature has been combined with data on biometrics, primary moult and recaptures to classify Knots as islandica or canutus. Others have worked in the same way. However, the reliability of these methods is not clear. Differences in the measurements are small and recoveries of ringed birds do not always support what the other data suggest. Not all of the recoveries, listed in Table 3, fit with the three groups identified above. Prokosch (1988) states that in spring *islandica* occurs in the German Wadden Sea up to 10 May and that later *canutus* occurs. This is inconsistent with the adult ringed at Holwerd on 29 July 1980 and recovered in the German Wadden Sea on 19 March 1987 (Arnhem K 571.379, Table 3). On the basis of its recovery date and place, it should have been islandica, but when caught at Holwerd, it was not in primary moult and should therefore have been canutus. The other recoveries in Table 3 are all consistent with *canutus*, but it is quite possible that some *islandica* occur at Holwerd among them.

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