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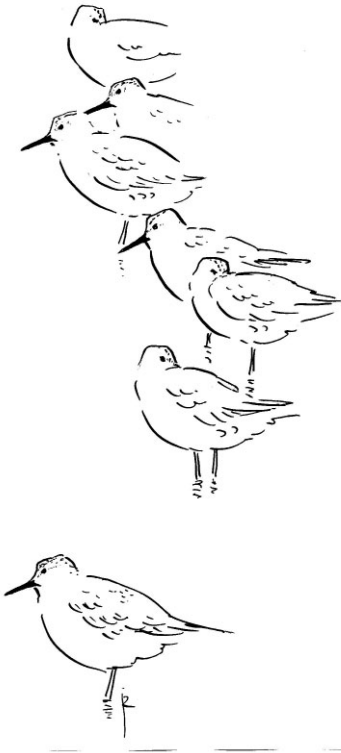
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Southward migration and fuel deposition of Red Knots *Calidris canutus*

Anders Helseth^{1,*}, Åke Lindström^{1,2} & Martin Stervander¹

Helseth A., Lindström Å. & Stervander M. 2005. Southward migration and fuel deposition of Red Knots *Calidris canutus*. *Ardea* 93(2): 213–224.



We compared the differences between spring and autumn in migration speed, fuelling rates and fuel loads of migrating Red Knots *Calidris canutus*. As a basis we used ringing data from Ottenby Bird Observatory, southeastern Sweden, collected 1948–2003, with morphometrical data from 1990–2003. Numbers ringed varied between 0 and 301 per year (average 56). Morphometrics, recoveries and recaptures of ringed birds indicated that most birds belonged to the Afro-Siberian subspecies *C. c. canutus*, possibly mixed with some Nearctic Red Knots *C. c. islandica*. Median trapping dates were 5 August (adults) and 31 August (juveniles). Mean body masses were low and almost equal for adults (111.8 g) and juveniles (111.4 g). The mean estimated fuel loads were 13–14% of lean body mass (LBM). In juveniles fuel loads increased with date. Among the few birds stopping over for longer than one day (2% of adults, 14% of juveniles), adult birds stayed on average 2.5 days and juveniles 3.4 days, with an overall average fuel deposition rate of 2.8% of LBM d⁻¹. The autumn migration speed was estimated from ringing recoveries at 86 km d⁻¹, which equals the speed of spring migration calculated from published information. The observed fuelling rate was as high as that of Red Knots at major spring stopover sites. We conclude that migration in autumn is as fast as in spring, although the generally small fuel loads indicate that migration is carried out in much smaller steps.

Key words: migration speed, ringing recoveries, morphometrics, shore-birds

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INTRODUCTION

The Red Knot *Calidris canutus* is one of the most impressive long-distance migratory waders and also one of the best studied. Particular focus has been given to the northbound (spring) migration. Red Knots then typically use only a few traditional stopover sites where they prepare for very long

flights (up to 6 900 km non-stop) towards the breeding grounds (Morrison 1975, Davidson & Evans 1986, Dick *et al.* 1987, Uttley *et al.* 1987, Gudmundsson *et al.* 1991, Piersma & Davidson 1992, Baker *et al.* 2004, Piersma *et al.* 2005). Not only do the birds add substantial fat loads, they also re-build muscles and organs to become efficient flyers (Piersma *et al.* 1999, Lindström *et al.*

2000). Red Knots generally stay for weeks at the same sites and increase in body mass by about 40–60% above lean body mass (LBM) at a rate of about 1–3% of LBM d^{-1} (Gudmundsson *et al.* 1991, Piersma *et al.* 2005).

The southward (autumn) migration of Red Knots has received less attention. It is generally acknowledged to be more extended in time than in spring, divided into several shorter flights and with a less concentrated use of stopover sites (e.g. Wilson & Morrison 1992). Body mass patterns during autumn migration are also relatively poorly known (Davidson & Wilson 1992, Piersma *et al.* 1992, Nebel *et al.* 2000). The body masses reported from the autumn have in general been much lower than in spring (Dick & Pienkowski 1979, Johnson 1985, Buxton 1989, Davidson & Wilson 1992, Morrison & Harrington 1992, Piersma *et al.* 1999), suggesting different migration strategies in spring and autumn. The most noteworthy exceptions are the high body masses of birds involved in trans-Atlantic flights from North to South America (McNeil & Cadieux 1972, Morrison & Harrington 1992).

Migration speed (measured in $km d^{-1}$) is the speed at which migratory birds cover their journey, including the periods spent on fuelling before and between the migratory flights (Alerstam & Lindström 1990). Especially for birds selected to minimize the time spent on migration ('time-minimizers'; Alerstam & Lindström 1990), migration speed is an important currency. Alerstam *et al.* (in press) reviewed studies where migration speed has been compared for spring and autumn in the same populations. In most cases, but not all, spring migration was faster than autumn migration. This pattern is not surprising given that arriving to the breeding grounds before competitors should have a strong selective advantage (Alerstam & Lindström 1990).

Hildén & Saurola (1982) found that migration speeds of arctic waders passing Finland in autumn were high, with Red Knots migrating on average 83 $km d^{-1}$. The highest speed recorded in an individual was 177 $km d^{-1}$, measured over 11 days (Hildén & Saurola 1982). Spring migration speed

in Nearctic Red Knots *C. c. islandica* migrating from the North Sea area to NE Canada, as estimated from start of fuelling to arrival at the breeding grounds (Davidson & Wilson 1992), is about 85 $km d^{-1}$. The corresponding value for Afro-Siberian Red Knots *C. c. canutus*, migrating from West Africa to Taimyr (Piersma *et al.* 1992), is about 90 $km d^{-1}$. Thus, it seems as if the spring and autumn migration may be carried out at about the same speed.

One important prerequisite for fast migration is a high fuelling rate (Alerstam & Lindström 1990). The data available indicate that fuelling rates in autumn may be as high as in spring, that is 2–3% of LBM d^{-1} (Gromadzka 1992, Meissner 1992, Morrison & Harrington 1992, Wilson & Morrison 1992, Nebel *et al.* 2000), but information is still scant. The main aim of the present study is to compare the migration strategy of Red Knots in spring and autumn, with particular focus on migration speed and patterns of fuel deposition. As a basis we use data from Ottenby Bird Observatory, where waders have been studied for nearly 60 consecutive years.

Several published accounts have dealt with the numbers, phenology and morphometrics of waders at Ottenby (Mascher & Marcström 1976, Holmgren *et al.* 1993a, b, Waldenström & Lindström 2001, Blomqvist *et al.* 2002, Hedenström 2004, Helseth *et al.* 2005). As far as Red Knots are concerned, already Kolthoff (1896) described that adults in general passed a month earlier in autumn than juveniles. Migration counts from the southward passage in 1947–1956 showed great inter-annual variation, with a mean number of 955 Red Knots per season (range = 338–2032, SD = 524.7; Edelstam 1972). Ringing has been carried out at Ottenby during autumn since 1946. Blomqvist *et al.* (2002) analysed Red Knot ringing data and found that adults pass mainly in early August and juveniles mainly in late August – early September. They also found that in years when predation pressure from foxes had been low on the Siberian breeding grounds, adults passed later in autumn, and more juveniles were trapped. Data on fuelling rates at Ottenby have not yet been published for



Figure 1. Recoveries of Red Knots *Calidris canutus* ringed in autumn at Ottenby, Sweden ($n = 56$), or ringed elsewhere and recaptured in autumn at Ottenby ($n = 8$, indicated by *). The symbols indicate the period during which a bird was found. Figures near symbols indicate the number of recaptured birds in the same area. The arrow shows the location of Ottenby.

Red Knots, but several other wader species trapped in autumn at Ottenby have been found to have remarkably high fuelling rates (Waldenström & Lindström 2001, Hedenström 2004, Helseth *et al.* 2005).

We present data on body mass, stopover length and fuel deposition rates of Red Knots trapped during autumn migration at Ottenby. We also analyse ringing recoveries of Red Knots to investigate to what extent the two subspecies occurring in the Western Palearctic, *canutus* and *islandica*, occur at Ottenby. Individuals of the two subspecies are difficult to separate on morphometrics and plumage alone, especially if the birds have not been sexed (Tomkovich 1992, Tomkovich & Soloviev 1996, Engelmoer & Roselaar 1998, Nebel *et al.* 2000). Given the easterly position of Ottenby within the East Atlantic Flyway it has been implicitly assumed that the Red Knots passing Ottenby in autumn belong to the subspecies *canutus* (Blomqvist *et al.* 2002), but *C. c. islandica* do occur in Sweden during spring migration (Blomqvist & Lindström 1992), and may possibly occur at Ottenby also in autumn.

METHODS

Trapping and ringing

Ottenby Bird Observatory (56°12'N, 16°24'E) is located on the southern point of Öland, an island in the Baltic Sea, southeastern Sweden (Fig. 1). The observatory was founded in 1946, but the first waders were ringed nearly ten years earlier, during two pilot-study seasons (Bergström & Svårdson 1938). The wader trapping is still one of the main activities and the trapping has been consistent throughout as far as the type and number of traps and yearly period of trapping are concerned (Waldenström & Lindström 2001, Blomqvist *et al.* 2002). Trapping starts in early July and continues to mid or late September and sometimes later, depending on the numbers of staging waders in the area. Between 80 and 120 traps of the so-called 'Ottenby-model' (a variant of walk-in funnel traps, see Bub 1991) are used. The cages are checked every full hour from dawn to dusk. Trapped birds are brought in cloth bags to the ringing laboratory (within 200 m of the traps) where they are processed and thereafter released.

Ageing and morphometrics

Red Knots in early autumn are easily aged as either juvenile (first calendar year bird) or adult (second calendar year or older) on plumage characters (Prater *et al.* 1977). Since 1990 the birds have been weighed to the nearest 0.1 or 1 g, using either an electronic balance or a Pesola spring balance. Birds recaptured one day or more after ringing were processed in the same way. No blood samples have been taken for molecular sexing and no birds were assigned to subspecies at ringing.

The lean body mass (LBM) was estimated at 99 g for adults and 98 g for juveniles, by averaging the 20% lowest body masses respectively recorded in each group, arbitrarily assuming that these birds represent a lean state. It should be stressed that the value given is an average and that there is variation in LBM between individuals. Accordingly, estimates of fuel loads and deposition rates of individual birds may be imprecise, whereas population averages should be more adequate.

Wing length was measured to the nearest 1 mm as maximum chord (flattened and straightened wing; Svensson 1992) and total head length was measured to the nearest 1 mm from tip of bill to back of skull (Green 1980).

Average migration speed was derived from all birds ringed and recovered during the same autumn. Recoveries of presumably wintering birds (dating from December or later) as well as recoveries of uncertain finding date were excluded. The average migration speed, which includes the fuelling periods, was calculated by dividing the total sum of distance covered by all birds with the total sum of days which had passed between ringing and recovery. This is in accordance with 'method B' used by Hildén & Saurola (1982). Means are given \pm SD.

RESULTS

Ringling and timing of passage

During southward migration at Ottenby, Red Knots most often appeared in small groups of 1–5 birds, but regularly also in multiples of tens. The highest

maximum daily figure we found in the Ottenby diary is 180 birds on 1 August 1992 (a day when 87 birds were ringed).

During 1948–2003, a total of 3037 Red Knots on autumn migration were ringed. Almost all birds (98%) were aged: 1883 as adults and 1089 as juveniles. The annual ringing figures of Red Knots at Ottenby varied between 0 (1968 and 1984) and 301 (1992), with an annual average of 56 (\pm 63.7). On average 34 adults (\pm 52.0) and 19 juveniles (\pm 32.4) were trapped per year. The median capture date of adult birds was 5 August and for the juveniles 31 August. For more information about variation in the number of birds ringed, see Blomqvist *et al.* (2002).

Morphometrics and stopover behaviour

The average wing length was 169.4 mm for adult Red Knots (\pm 4.0, range = 155–181, n = 584) and 163.2 for juveniles (\pm 3.7, range = 150–172, n = 102). The wing length of adults decreased significantly with time, equal to about 1.6 mm over a one-month period (regression coefficient b = -0.055, r^2 = 0.013, P = 0.006). No significant change occurred in juveniles (b = 0.061, r^2 = 0.015, P = 0.22). The average total head length was 63.9 mm for adults (\pm 2.1, range = 54–69, n = 543) and 62.0 mm for juveniles (\pm 2.1, range = 55–62, n = 99). The head length of adults decreased significantly within a season (b = -0.027, r^2 = 0.009, P = 0.025) while no significant trend was found in juveniles (b = -0.039, r^2 = 0.024, P = 0.13).

The mean body mass was 111.8 g for adult birds (\pm 9.5, range = 80–145, n = 575) and 111.4 g for juveniles (\pm 13.6, range = 92–174, n = 100). The average body mass in adults did not change over season (b = -0.07, r^2 = 0.003, P = 0.17, n = 575), but increased significantly in juveniles (b = 0.70, r^2 = 0.151, P < 0.001, n = 100; Fig. 2). The average overall fuel load (as a proportion of the estimated LBM) was 13.0% for adults and 13.7% for juveniles. The highest estimated fuel load, 77.2%, was recorded in a juvenile bird.

During 1990–2003, 25 birds (11 adults and 14 juveniles) were recaptured at Ottenby one day or

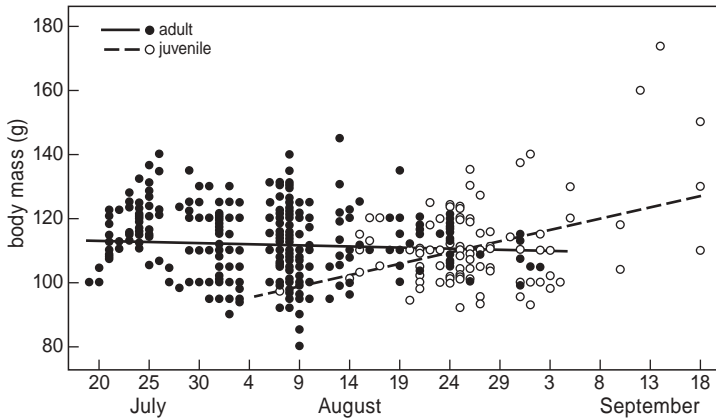


Figure 2. Body mass over season in Red Knots *Calidris canutus* ringed at Ottenby, Sweden, 1990–2003 (excluding retraps). The trend is statistically significant in juveniles but not in adults.

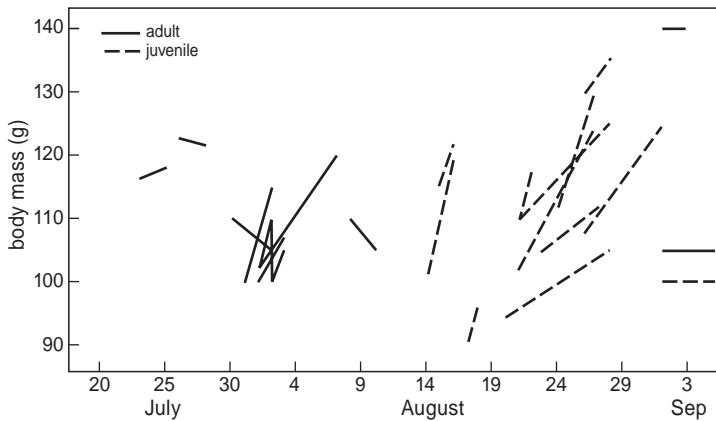


Figure 3. Changes in body mass over time in recaptured Red Knots *Calidris canutus* at Ottenby, Sweden, 1990–2003. Data are given for adults ($n = 11$) and juveniles ($n = 14$) separately. For birds recaptured more than once, only the body mass of the last trapping occasion is given.

more after ringing and within the same season (Fig. 3). During the same period 586 adults and 103 juveniles were ringed, implying that 2% of the adults and 14% of the juveniles were retrapped. The average number of days between ringing and last retrap was 3.0 (range 1–8 days). This interval was on average 2.5 days in adults and 3.4 days in juveniles, but with no statistically significant difference between the age groups (unequal variances t-test, $t_{21.6} = 1.24$, $P = 0.23$).

The body mass change was positive for 21 of the 25 recaptured birds (84%). The overall average mass change was 2.8% of LBM d^{-1} (range -5.1 to 9.3%, $n = 25$). There was no significant effect of stopover length on fuel deposition rate, nor was there a difference between the age groups (ANCOVA, effect of stopover length, $F_{1, 22} = 2.0$,

$P = 0.17$, effect of age, $F_{1, 22} = 2.6$, $P = 0.12$; an insignificant interaction term was excluded; Fig. 4). If anything, there was a tendency that overall fuel deposition rate decreased with length of stay.

Migration routes and migration speed according to ringing recoveries

In total, 56 Red Knots (23 adults, 32 juveniles and one with unspecified age) ringed at Ottenby have been recovered elsewhere, and eight birds ringed elsewhere have been recaptured at Ottenby (Fig. 1). There have been no recoveries from June or from potential breeding grounds, but two birds ringed in Finland on autumn migration have been recaptured at Ottenby the same autumn, indicating an eastern origin. The majority of the recoveries and recaptures originate from the Atlantic coast

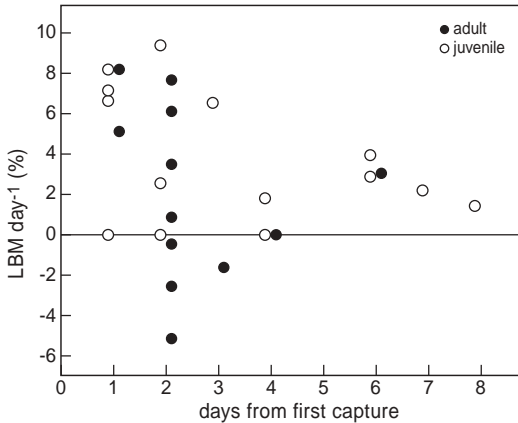


Figure 4. Fuel deposition rate (percentage of lean body mass (LBM) per day) in relation to the interval between two catches in Red Knots *Calidris canutus* at Ottenby, Sweden, 1990–2003. Data are given for adults ($n = 11$) and juveniles ($n = 14$) separately. For birds recaptured more than once, fuelling rate is only given for the period up to the last trapping occasion.

in Europe, but three were made in western Africa. In addition, one bird ringed in Langebaan Beach roost, Cape Province, South Africa, 10 March 1984 was recaptured at Ottenby 27 July 1988.

Seven winter records of Red Knots ringed at Ottenby come from England, Scotland, Germany and France, of which two were juveniles in their first winter and five adults.

The average autumn migration speed was 85.8 km d^{-1} ($n = 26$). The highest speed recorded was 366 km d^{-1} , measured over three days.

DISCUSSION

Which subspecies of Red Knots pass Ottenby in autumn?

According to Engelmoer & Roselaar (1998), the differences in bill and wing length between *C. c. canutus* and *C. c. islandica* are small and, accordingly, useless for subspecies recognition. However, Tomkovich & Soloviev (1996) found *canutus* at their breeding grounds to clearly have longer bills and shorter wings than birds assigned to *islandica*

in various studies. Further, Nebel *et al.* (2000) used bill length as a marker of subspecies identity in molecularly sexed individuals in their study of autumn migrating Red Knots in the Wadden Sea. Meissner & Kamont (2005) found that autumn migrating Knots at the Polish Baltic coast had measurements strongly resembling those of the *canutus* subspecies, and differing from known *islandica* birds.

The averages of wing and total head length in adults were very similar to those measured by Meissner & Kamont (2005) in Poland (wing length 169.4 vs. 169.7 mm, total head length 63.9 vs. 63.6 mm) strongly indicating that also Ottenby is mainly visited by the *canutus* subspecies.

We found negative trends over time in both wing and head length of adults (the same pattern was found in Poland, Meissner & Kamont 2005). Shorter wings later in the autumn could be due to wear of the tips of the longest primaries, but juveniles showed no negative trend with time. More likely, the pattern reflects the gradual change in the proportion of birds belonging to different sexes. The more long-billed and long-winged females depart earlier from the breeding grounds than the males (Tomkovich & Soloviev 1996).

There are additional good reasons to believe that the majority of the Red Knots passing Ottenby during southward migration belong to the subspecies *canutus*. First, some recoveries and recaptures involve western and southern Africa. Only *C. c. canutus* are known to winter in Africa. In addition, given the much lower likelihood of getting recoveries from Africa than Europe, the proportion (6.3%) of the African recoveries and recaptures must be seen as high. Second, two birds ringed in Finland and recaptured at Ottenby the same autumn also suggests an eastern origin. Third, although no less than 100 651 Red Knots have been ringed in the United Kingdom 1945–2003, not a single bird has been recaptured at Ottenby (J. Clark, pers. comm.). Red Knots in the UK belong to the subspecies *islandica* (Boyd & Piersma 2001, Davidson 2002), and if these *islandica* birds move as far east as the Baltic Sea, we would expect to have recaptured some of them at

Ottenby. This pattern is in sharp contrast to the Dunlin *Calidris alpina*, where at least 554 of the 414 219 birds ringed in the UK have been recaptured at Ottenby (J. Clark, pers. comm.). Fourth, there is strong correlation between the lemming cycles in Siberia and the numbers and timing of Red Knots at Ottenby (Blomqvist *et al.* 2002).

Nevertheless, there are seven winter recoveries from Western Europe, which indicate that, along the lines of reasoning above, some birds ringed at Ottenby could belong to the subspecies *islandica*. These observations are paralleled by winter recoveries from Western Europe of Red Knots ringed elsewhere in the Baltic: in northern Poland, (nine birds, Gromadzka 1992), and in Wismar Bay in Germany (two birds, Nehls 1987). There are good reasons to believe that *C. c. islandica* pass Ottenby during the spring migration (Blomqvist & Lindström 1992).

We conclude that the majority of Red Knots at Ottenby belong to *C. c. canutus*, and that some birds may belong to *C. c. islandica*. We cannot exclude the possibility, however, that all birds at Ottenby belong to *C. c. canutus*, and that some *canutus* birds stay in Western Europe during the winter

Timing of passage

The median spring passage date at Ottenby for *C. c. canutus* was 8 June (Blomqvist & Lindström 1992). On average two months later (5 August) the adult Red Knots pass Ottenby again on their southward migration. In this short time period the Red Knots should fly to the breeding areas, lay eggs, incubate, raise the young and migrate back again.

However, the average passage time at Ottenby varies between years. Blomqvist *et al.* (2002) found that the autumn passage of adult Red Knots at Ottenby was earlier in years when nest predation pressure was high and breeding unsuccessful, compared to years when predation pressure was low and more young were produced. Thus, a proportion of the adults passing Ottenby each year are failed breeders that probably left the breeding grounds before successful breeders, leading to an

underestimate of the time needed to carry out a complete breeding cycle.

The difference between the median passage date of adult and juvenile Red Knots was 26 days, which is similar to the situation in the Gulf of Gdansk, northern Poland, where adult Red Knots migrate about one month earlier than juveniles (Meissner 1992). Similar differences in migration peaks are seen in other waders at Ottenby; 33 days for Curlew Sandpipers *Calidris ferruginea* (Blomqvist *et al.* 2002), 27 days for Broad-billed Sandpipers *Limicola falcinellus* (Waldenström & Lindström 2001) and 23 days for Temminck's Stints *Calidris temminckii* (Hedenström 2004), though only 10 days for Ruddy Turnstones *Arenaria interpres* (Helseth *et al.* 2005).

Body mass, fuel deposition and migration speed

An average body mass of around 110 g in adults and juveniles is very low compared to the averages of 190–210 g in adults prior to departure from spring migration staging sites around the world (Gudmundsson *et al.* 1991, Piersma *et al.* 2005). This strongly suggests that this part of the autumn migration is carried out in much shorter steps than in spring.

Low mean body masses in autumn have been reported from Scotland (94 g; Buxton 1989), England (120–140 g; Johnson 1985, Wilson & Morrison 1992), Poland (90–120 g; Gromadzka 1992, Meissner 1992, Meissner & Kamont 2005), northwest Africa (100–120 g; Dick & Pienkowski 1979), and Iceland (130–140 g; Wilson & Morrison 1992, Piersma *et al.* 1999). In only some of these cases body mass was low because the birds just completed long over-water flights. Further, at none of these sites are there indications of substantial fuelling. Accordingly, a general pattern of lean birds on southward migration emerges. However, Red Knots involved in long trans-ocean flights between North and South America carry substantial fuel loads (body mass of 180 g; McNeil & Cadieux 1972, Morrison & Harrington 1992), showing that a low autumn body mass in Red Knots is not universal. Nebel *et al.* (2000) recorded body masses in the Wadden

Sea in autumn of about 140–180 g and suggested that departure masses regularly reached 200 g, representing another example of possible long non-stop flights in autumn.

Several studies have estimated lean body mass of Red Knots in spring to amount at about 135 g (Johnson 1985, Gudmundsson *et al.* 1991, Piersma *et al.* 1999). This is much higher than the autumn mass of 100–110 g reported here, as well as in other autumn studies. Nevertheless, in none of the autumn studies were birds considered starving or in bad condition. Many actually rapidly gained mass, indicating good health (Buxton 1989, Gromadzka 1992, Meissner 1992, Wilson & Morrison 1992, this study). The low body mass found therefore most likely mirrors generally smaller protein stores, that is, smaller muscles and organs. It is well known that migrants in general (Piersma & Lindström 1997, Piersma & Gill 1998, Battley *et al.* 2000), and Red Knots in particular (Piersma *et al.* 1999, Lindström *et al.* 2000, van Gils *et al.* 2003) have a remarkable flexibility regarding the size of muscles and organs in relation to their ecological needs.

The factors selecting for small muscles and organs in autumn are not known, but one reason could be that the shorter flight steps chosen require no heavy fuel loads and thus no corresponding development of flight muscles, as during spring migration (Piersma *et al.* 1999). Another reason could be that the diet during spring and autumn migration differs. During spring migration, Red Knots often forage on marine molluscs and bivalves (Alerstam *et al.* 1992), demanding a large gizzard (van Gils *et al.* 2003), but there are exceptions (Baker *et al.* 2004). In autumn at Ottenby, the birds are not feeding on shellfish, rather on soft-bodied food like fly larvae (own observations), with no need for a large digestion apparatus. How general this pattern is in autumn we do not know, and certainly when arriving at the Wadden Sea, the birds would need to adapt to hard-bodied prey (van Gils *et al.* 2003).

Body masses were almost identical for adult and juvenile Red Knots at Ottenby, as was the case in Poland (Gromadzka 1992, Meissner & Kamont

2005). Similarity in body mass between age groups has been found at Ottenby also for Broad-billed Sandpipers (Waldenström & Lindström 2001), Temminck's Stints (Hedenström 2004) and Ruddy Turnstones (Helseth *et al.* 2005).

The few adults recaptured more than one day after first capture stayed on average 2.5 days, whereas juveniles stayed 3.4 days. In the Gulf of Gdansk, northern Poland, adults stayed on average 1.8 days while juveniles stayed 4.0 days (Meissner 1992).

The fuel deposition rate during stopover at Ottenby was on average 2.8%, with an individual maximum 9.3% of LBM d^{-1} . The average is in accordance with other studies both in spring (Gudmundsson *et al.* 1991, Piersma *et al.* 2005) and autumn (Meissner 1992, Nebel *et al.* 2000). Lindström (2003) reviewed published information on the fuel deposition rates of migrating birds and calculated allometries based on the highest species averages and highest individual values, respectively. Based on these allometries the population average for Red Knots at Ottenby with a 98 g LBM (see Methods) can be expected to be 2.6% of LBM day^{-1} with individual rates up to 4.8% of LBM day^{-1} . Obviously, the values we found show that Red Knots at Ottenby on average seem to encounter food situations allowing as high fuelling rates as Red Knots at other preferred stopover sites, and as individuals of other similar-sized migratory species. Still, they are far from the physiological maximum. Kvist & Lindström (2003) showed that Red Knots on autumn migration at Ottenby, given food access *ad libitum* in captivity, could increase their body mass with on average 13.4% of LBM d^{-1} .

High fuelling rates enable fast migration (Alerstam & Lindström 1990). Therefore, the high fuelling rates of waders at Ottenby are in line with the fast migration through northern Europe by arctic waders in autumn (Hildén & Saurola 1982, Alerstam & Lindström 1990). The overall autumn migration speed of Red Knots seems to be just as high as the average spring migration speed, around 80–90 km d^{-1} , as estimated from ringing recoveries in autumn (Hildén & Saurola 1982, this

study) and calculated from data on start of fuelling and arrival to the breeding grounds in spring (data from Davidson & Wilson 1992, Piersma *et al.* 1992, see Introduction). As fuelling rates are similar in spring and autumn, the main difference in migration strategy lies in the amount of fuel put on. In autumn the birds rarely stage for longer periods and the migratory fuel loads are comparatively small, despite the apparently favourable food situation. Such a scenario, with small fuel loads and (by necessity) short flights can be expected for time-minimizers when there are low or no search or settling costs when arriving to new staging sites and/or continuously high fuelling rates further along the route can be expected (Alerstam & Lindström 1990, Lindström & Alerstam 1992).

An equal migration speed in spring and autumn seems to be relatively uncommon (Alerstam *et al.* in press), and not in line with the assumption that the premium on fast migration is highest in spring. However, from the fact that migration speed is equal in spring and autumn in Red Knots does not immediately follow that the selection on early arrival to stopover, moult or wintering sites during southward migration is as high as on early arrival to the breeding grounds in spring. The actual conditions along the migratory route can be very different in spring and autumn and accordingly, the potential migration speed can be different. For example, should food abundance at the stopover sites for a given species on average be much higher in autumn than in spring, but migration speed is the same, we could conclude that the birds are more relaxed during autumn migration (they do not make use of the higher potential fuelling rates).

The estimated autumn migration speed 83–86 km d⁻¹ (Hildén & Saurola 1982, this study) corresponds to an average of about 1.5 h active flight per day (assuming a flight speed of 60 km h⁻¹). Red Knots lose around 0.75% of body mass per hour of flight (own observations). Accordingly, a 110 g bird loses on average 1.2 g, that is 1.2% of LBM, per day while flying. However, the Red Knots while staging at Ottenby gain on average as much

as 2.8% of LBM d⁻¹, which is considerably more than needed to make up for the fuel lost in flight. Over the migration period these two figures should match. We can only speculate about the reason for this discrepancy. Ottenby may be an unusually good site, that is, fuel deposition rates are higher than at other sites. For example, if two other stopover sites visited allow a fuel deposition rate of only 0.4%, the overall average fuel deposition rate would be 1.2% $([2.8 + 0.4 + 0.4]/3)$. That fuelling rates can vary drastically between stopover sites along the migration route has been shown for Red Knots during northward migration (Piersma *et al.* 2005). Another possible explanation for the apparent discrepancy between migration speed and fuelling rate is that some of the estimates are imprecise.

An interesting phenomenon at Ottenby is that fuel loads tend to increase during the season in juvenile Red Knots, but not in adults which migrate earlier in autumn (as found in Poland, Meissner & Kamont 2005). Meissner & Kamont (2005) proposed that late and heavier birds might be more time-selected than early birds. This may be true, but information about fuel stores alone is not enough to conclude this. The optimal fuel load for time-selected migrants depends on the one hand on the distance to the stopover sites ahead and on the other hand on the quality of these sites (Gudmundsson *et al.* 1991). Assuming that Red Knots always are time-minimizers, the pattern can be explained if the stopover sites southwest of the Baltic become poorer than Ottenby with the progress of season. Alternatively, late juveniles may put on larger energy stores in preparation for poor weather conditions to be expected in the course of autumn. That is, the stores are not only to fuel for migratory flights but also for short-term survival.

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SAMENVATTING

De Kanoet *Calidris canutus* is een van de indrukwekkendste en best bestudeerde langeafstandstrekkingen. In dit stuk vergelijken de auteurs het verschil in treksnelheid, opvetsnelheid en hoeveelheid vetreserves van Kanoeten tijdens de najaarstrek in Zweden met die tijdens de voorjaarstrek. Hiertoe gebruiken ze ringgegevens (1948–2003) van het ringstation op Ottenby in Zuidoost-Zweden, gecombineerd met morfometrische gegevens van dezelfde locatie (1990–2003). Het aantal geringde vogels per jaar varieerde van 0 tot 301 (gemiddeld 56). Morfometrische gegevens, terugvangsten en terugmeldingen van geringde vogels laten zien dat de meeste Kanoeten die langs Ottenby trekken behoren tot de Afro-Siberische ondersoort *C. c. canutus*, al sluiten de auteurs niet uit dat enkele vogels van de ondersoort *C. c. islandica* zijn. De mediaan van de vangdata tijdens de zuidwaarts gerichte najaarstrek was 5 augustus voor adulte en 31 augustus voor juveniele vogels. Gemiddelde lichaamsgewichten waren laag en bijna identiek voor adulte (111,8 g) en juveniele vogels (111,4 g). De gemiddelde geschatte vetreserves besloegen 13–14% van

het vetvrije lichaamsgewicht. De vetreserves van juveniele vogels namen toe met de datum: later doortrekkende jongen waren zwaarder dan eerder doortrekkende individuen. Van de Kanoeten die meer dan één dag op Ottenby verbleven (2% van de adulte vogels, 14% van de juveniele vogels) bleven de adulte vogels gemiddeld 2,5 dagen en de juveniele vogels gemiddeld 3,4 dagen. Tijdens deze periode was de dagelijkse opvetsnelheid gemiddeld 2,8% van het vetvrije lichaamsgewicht. Daarmee is de opvetsnelheid in het najaar zeer vergelijkbaar met de opvetsnelheid van Kanoeten in het voorjaar op belangrijk tussenstoplocaties. De treksnelheid in het najaar, geschat met behulp van terugmeldingen, was 86 km per dag, bijna identiek aan eerder gepubliceerde schattingen van de treksnelheid van Kanoeten in het voorjaar. De voornaamste conclusie van de auteurs is dat Kanoeten tijdens de najaarstrek net zo snel vliegen als tijdens de voorjaarstrek, maar dat de kleinere vetreserves erop wijzen dat de najaarstrek is opgedeeld in kortere etappes dan de voorjaarstrek. (BIT)

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