Stopover Strategy of Adult and Juvenile Red Knots Calidris c. canutus in the Puck Bay, Southern Baltic

Author: Meissner, Włodzimierz

Stopover strategy of adult and juvenile Red Knots *Calidris c. canutus* in the Puck Bay, southern Baltic

Włodzimierz Meissner[1]

For Red Knots *Calidris c. canutus* sandy coasts of the southern Baltic seem to be a low quality stopover site, because of unpredictable feeding conditions and a low density of molluscs. Observation collected in the Puck Bay, Poland, suggest that Knots feed mainly on *Nereis* sp., *Gammarus* sp., small sized *Hydrobia* sp. and small insects taken from wet sand. Among 1471 Knots ringed 27.8% of juveniles and 10.5% of adults were retrapped few days after the first capture, which indicates that the majority had a short stay and apparently departed with small energetic reserves. In spite of poor feeding conditions the fuel deposition rate of the Knots in autumn (adults: 2.4 g per d, juveniles: 2.7 g per d) was similar to that observed in the Dutch Wadden Sea and the Baltic coast of SE Sweden. It is suggested that Knots are able to accumulate body stores despite low food quality and density because the lack of tides allow them to forage without interruption, and because there is no additional energetic cost related to increasing gizzard size.

Key words: Knot, southern Baltic, autumn migration, stopover strategy

[1]Avian Ecophysiology Unit, Department of Vertebrate Ecology & Zoology, University of Gdańsk, Al. Legionów 9, 80-441 Gdańsk, Poland; (w.meissner@univ.gda.pl)
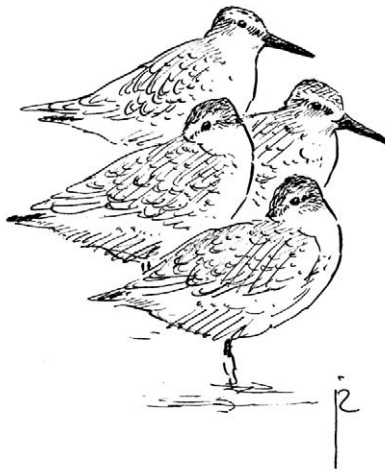
INTRODUCTION

The occurrence of Knot *Calidris canutus* outside the breeding season is restricted to soft-sediment intertidal areas, where it mainly feeds on small molluscs. Red Knots *C. canutus canutus* appear only during autumn migration towards African wintering grounds in the Baltic region (Meissner 2005a). This species undertakes long-distance flights between the arctic breeding grounds and temperate or tropical wintering areas (Piersma & Davidson 1992), and for fast refuelling it needs to stop in sites with high densities of benthic invertebrates (Piersma *et al.* 1992). The sandy coasts of the southern Baltic represent a low quality habitat for migrating Knots, where the birds might encounter difficulties to find sufficient food to meet energy demands. Bivalves, which are the main prey of Knot outside the breeding period, are inaccessible for most of the time due to a lack of regular tides. Even when the water level drops during periods of strong wind and the bottom in shallowest places is exposed, the density of molluscs within reach of the waders is much lower than in the Dutch Wadden Sea (Piersma *et al.* 1993, Kube 1994, Górecki 2003, Włodarczak-Komosińska 2004). Moreover, feeding conditions for waders on the Baltic coasts are very changeable and unpredictable due to variable water level (Kube 1994, Włodarczak-Komosińska 2004).

Additionally, invertebrates in the brackish water of the Baltic are smaller than their congeners in intertidal areas of the North Atlantic (Kautsky 1998). Furthermore, there is a strong competition from other waders, especially Dunlin *Calidris alpina* and Curlew Sandpiper *Calidris ferruginea*, which are numerous on the Baltic coasts at the same time. In mixed flocks Knots lose the majority of interspecific aggressive interactions even with smaller waders (Stawarczyk 1984).

The irregular occurrence of adult Knots and their very low body mass (Meissner 2005a, Meissner & Kamont 2005) indicate that the southern Baltic is rather an emergency feeding place, than a regular stopover site on the route from Siberia to Africa. The mean body mass of adult Knots caught in autumn in the southern Baltic is among the lowest reported for the subspecies *C. c. canutus* (Piersma *et al.* 1992, Meissner & Kamont 2005). Autumn records of juvenile Knots in the southern Baltic are dispersed along the migration route, and are less concentrated than adults at traditional stopover sites (Gromadzka 1992, Dierschke 1995). Thus, it is possible that juveniles migrate in small hops rather than in long-distance flights, as adults do, using the southern Baltic as one of many stopover sites along their migration route. If true, it might be expected that adults and juveniles behave differently in use of stopover sites.

The aim of this paper is to compare the stopover pattern of adult and juvenile Knots at the Polish Baltic coast in autumn, on their way towards the wintering grounds. Particular focus is on key features of stopover strategies, i.e. the length of stay and body mass changes.

METHODS

Studies were conducted between 1988 and 1995 in the western part of the Gulf of Gdańsk (Puck Bay), on the narrow sandy spit in Rewa village (Fig. 1). The length of the spit depended on water level and varied from c. 500 to 1000 m. Waders were caught and ringed on a regular basis, using walk-in traps (Meissner 1998). Fieldwork lasted
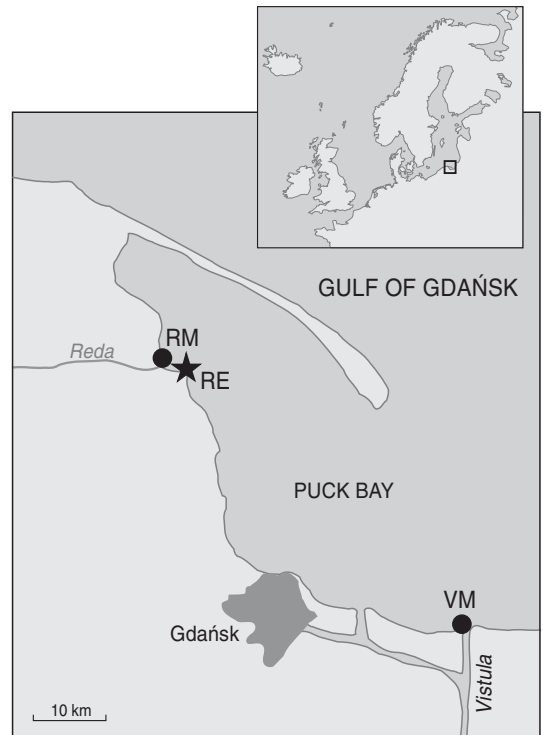

Figure 1. Location of the ringing site at Rewa (RE) and other places mentioned in the text: RM = Reda mouth, VM = Vistula mouth.

from mid-July through the end of September. This period covered almost the whole period of Knot migration in the study area (Meissner & Sikora 1995). In total, 1071 juvenile and 400 adult Knots were ringed. Each Knot was aged (Prater *et al.* 1977) and weighed with an accuracy of 1 g. Lengths were measured of wing, total head, bill and tarsus (Meissner 2000). To estimate energy reserves, it was necessary to correct for body size because the size of adults and juveniles decreased progressively through the season (Meissner & Kamont 2005). Among the measurements taken, the wing length in adults and total head length in juveniles showed the highest correlation coefficient with body mass ($r = 0.32$ and $r = 0.33$, respectively, both $P < 0.05$). However, wing length might vary within the season due to abrasion of

the longest primary (Pienkowski & Minton 1973), potentially affected by food quality during the moult (Pehrsson 1987). Therefore, both in juveniles and adults the total head length was used to correct body mass (correlation coefficient between total head length and body mass in adults $r = 0.29$, $P < 0.05$). The adjusted body mass of each bird was calculated from the residuals of the regressions of body mass on total head length for juveniles and adults.

Body mass changes were expressed as the difference between body mass at the first and subsequent captures. To obtain an instantaneous measure of the rate of body mass increase birds trapped within four days after first capture were selected. The length of stay was estimated using capture–recapture techniques following Schaub *et al.* (2001).

Along the coast of the Puck Bay only few sites are suitable for waders to feed. The most important ones are close to the river mouths of the Vistula and Reda (where the main study area was located). Within the study period, waders were also ringed at the mouth of the Vistula river (about 45 km apart in a straight line) (Gromadzka 1998). Some birds used only a single area, while others were recorded in both regions. During autumn migration the majority of wader movements within Puck Bay were directed from the eastern to the western part (Brewka *et al.* 1987). To show the intensity of passages of Knots within the Puck Bay, the Index of Direct Recoveries (IDR) between two ringing sites was calculated (Busse 1982). It was deduced from the number of recoveries per 100 birds ringed at one site and 100 birds caught at the second as:

$$IDR = \frac{V_{1-2}}{NR_1 \times NC_2} \times 10^4$$

where V_{1-2} = number of birds ringed at the ringing site 1 and recovered within the same season at ringing site 2, NR_1 = number of ringed birds at site 1, NC_2 = number of caught birds at site 2 (including retraps and recoveries). All other statistical methods followed Zar (1996). Analyses were done in STATISTICA 6.0 software (StatSoft 2001).

RESULTS

Number of retraps and length of stay

In total 298 (27.8%) juveniles were retrapped within the same autumn, and only 42 (10.5%) adults (comparing the percentages, $\chi^2 = 45.89$, $P < 0.0001$). The mean length of stay of adults (2.98 days) was about three times shorter than in juveniles (9.36 days).

Body mass changes

Two-way ANOVA indicated significant differences in mean adjusted body mass among years ($F_{7,1327} = 6.15$, $P < 0.0001$), but not age ($F_{1,1327} = 0.03$, $P = 0.86$) and not year-age interaction ($F_{7,1327} = 0.83$, $P = 0.56$; Fig. 2).

During the first four days after capture, juveniles exhibited a similar body mass increase among years (ANOVA, $F_{4,208} = 1.25$, $P = 0.29$). The number of retraps of adults was much lower and comparing two years with a reasonable sample size (1991 and 1995, when ten and eleven retraps occurred) indicated no year effect (*t*-test, $P > 0.05$). Thus, within each age class samples from all years were combined for subsequent analyses.

Knots from both age classes increased body mass significantly during their stay (Fig. 3).
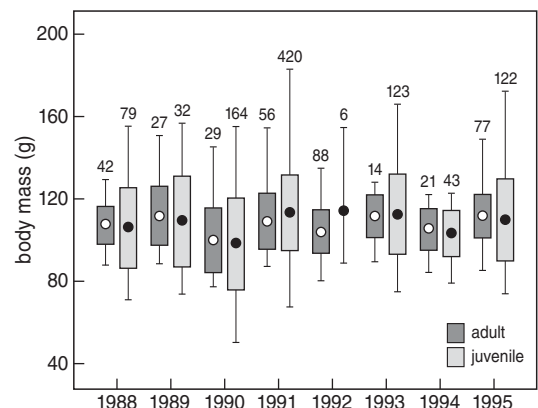

Figure 2. Changes in the adjusted body mass in adult and juvenile Knots caught in consecutive seasons. Indicated are mean, SD (box), range (whiskers) and sample size.
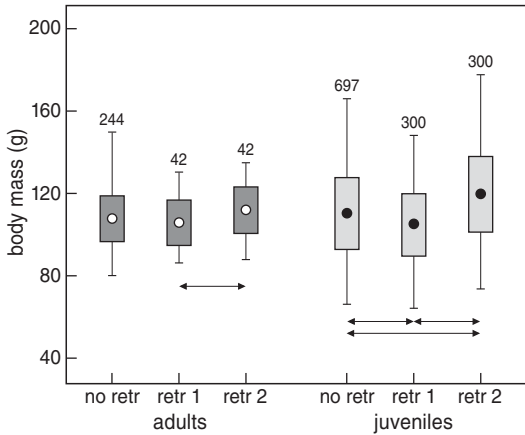
Figure 3. Comparison of mean body mass of Knots caught only once (No retr) and in retraps at the first (Retr 1) and the last capture (Retr 2) in adults (ANOVA, $F_{2,325} = 3.76$, $P = 0.002$) and in juveniles (ANOVA, $F_{2,1294} = 56.27$, $P < 0.0001$). Arrows indicate significant difference according to post-hoc Tukey test at $P < 0.05$. Indicated are mean, SD (box), range (whiskers) and sample size.

Juveniles that were retrapped had a lower body mass at first capture than birds caught only once. There was no such difference in adults (Fig. 3).

There were large differences among individuals in body mass increment. Some juveniles gained more than 60 g after 10 days, while others hardly changed their body mass after this period (Fig. 4). The overall body mass increase during the first four days was similar in adults (mean 2.4 g day^{-1} ± 3.70 SD, $n = 38$) and juveniles (mean=2.7 g day^{-1} ± 4.13 SD, $n = 223$; t-test, $t = 0.39$, $P = 0.70$). However, adults did not stay as long as juveniles and their body mass at last capture was on average about 7 g lower than that of juveniles (Cochran-Cox test, $t' = 3.55$, $P = 0.0007$; Fig. 3).

Juveniles which lost body mass during the first day after catching had a significantly higher adjusted body mass than birds that put on mass from the beginning onwards (Fig. 5) (t-test, $t = 3.20$, $P = 0.002$). Small sample sizes of retrapped adults did not allow a similar comparison, although the few data indicate a similar pattern as in juveniles; three adults which lost body mass
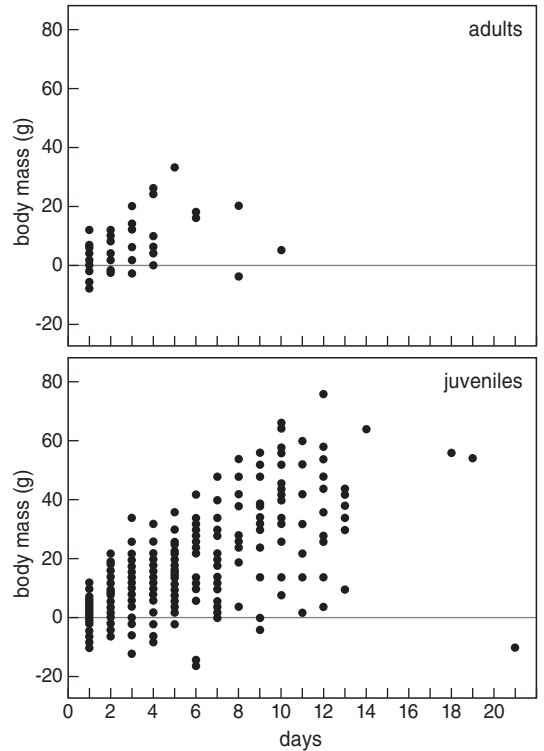

Figure 4. Changes in the body mass in following days between first and subsequent capture of adult and juvenile Knots retrapped in Rewa.
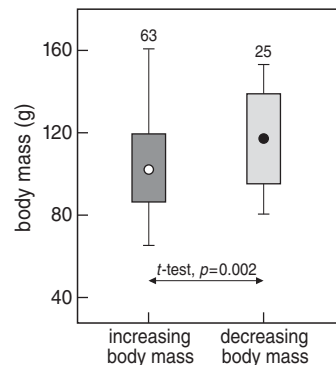

Figure 5. Mean adjusted body mass at first capture in juveniles increasing (dark grey) and loosing (light grey) weight after one day. Indicated are mean, SD (box), range (whiskers) and sample size.

during the first day after capture, weighed 112 g, 119 g and 134 g, which was much higher than the mean adjusted body mass of adults that increased their weight after one day (mean 101.0 ± 12.27 SD, $n = 12$).

Ringing recoveries

Between 1988 and 1995 movements of 16 juveniles and 4 adults between Vistula and Rewa were recorded. In juveniles the period between ringing at Vistula and recapture in Rewa ranged between 0 and 33 days (median 3). Five of them (31%) were retrapped after two days. In adults, three birds were recorded the same day at both sites, while the fourth was recorded at the second site after three days. The Index of Direct Recoveries between Vistula and Rewa was noticeably higher in adults (IDR = 0.67) than in juveniles (IDR = 0.29). In the opposite direction only one juvenile bird moved (IDR = 0.02).

Of the Knots ringed at Rewa, several were recovered at a distance of more than 100 km; 24 juveniles and 6 adults. This indicates recovery rates of 2.2% and 1.5%, respectively, which are not significantly different (χ^2-test, $\chi^2 = 0.82$, $P = 0.37$). Among these recoveries, six juveniles and one adult were retrapped in the western Baltic at the Langenwerder Island (450 km in a straight line from the study area) no later than after 9 days (one juvenile after 21 days), while other records came from the intertidal area of the North Sea and Atlantic.

DISCUSSION

Fuel deposition rates of adult Red Knots in the Puck Bay were similar to those observed in autumn in the Dutch Wadden Sea (2.8 g d^{-1}) and in the Baltic coast of SE Sweden (2.7 g d^{-1}, calculated for both age classes) (Nebel *et al.* 2000, Helseth *et al.* 2005). However, in the Wadden Sea Knots stay much longer than in the Baltic area and the departure body mass of adult females is estimated at about 200g (Nebel *et al.* 2000). During their stay at the southern Baltic coasts Knots spend

most of their time on foraging (Dierschke & Rippe 1997, own observations), similar to other *Calidris* species (Górecki 2003, Włodarczak-Komosińska 2004). They are able to accumulate fat stores despite low food quality and density because the lack of tides makes long periods of foraging without interruption possible. Another reason that Knots achieve a similar fuelling rate on poor quality Baltic sandy coasts as in rich intertidal mudflats might be the gizzard size, which in Knots varies considerably during the year (Dekinga *et al.* 2001, van Gils *et al.* 2005). After the breeding season the gizzard of Knots increases rapidly in response to a shift in diet from rather soft-bodied arthropods to hard-shelled molluscs (Dekinga *et al.* 2001, van Gils *et al.* 2005). These adjustments of digestive organs are important for permitting the high feeding rate during migration and wintering (van Gils *et al.* 2003, 2005). However, a large gizzard entails higher maintenance and transport cost and hence overall energetic costs increase with gizzard size (Piersma *et al.* 2003, van Gils *et al.* 2003). There are no empirical data on the gizzard size of Knots from Baltic stopover sites, but it is likely that birds arrive there directly from the breeding grounds (Meissner 2005a). Thus, when landing in the southern Baltic area, both adults and juveniles might still have a small stomach to increase later in tidal areas when the birds change diet to hard-shelled molluscs (Dekinga *et al.* 2001, Battley & Piersma 2005). This assumption is in agreement with data on small stomachs of Knots arriving in autumn in the Dutch Wadden Sea and *islandica* Knots making stopover in Iceland after leaving their breeding grounds (Battley & Piersma 2005). Data on stomach contents of two Knots obtained by stomach pumping in 2001 and observations of foraging birds also strongly suggest that they feed on the same prey as Dunlins in this area, e.g. *Nereis* sp., *Gammarus* sp., small sized *Hydrobia* sp. and different small insects taken from wet sand (A. Włodarczak-Komosińska, unpubl. data).

The percentage of retraps was lower and the mean length of stay was shorter in adults than in juveniles, and similar differences were found in other wader species in Puck Bay during autumn

migration (Meissner & Koziróg 2001, Meissner & Ściborski 2002, Meissner 2005b, Meissner & Górecki 2006). The very low number of retraps (Meissner 1992, this study) indicates that the majority of Knots probably departed with small energetic reserves after a short stay. However, some juvenile birds (especially those with small energetic reserves at arrival) stopped for few days and they were able to achieve a considerable gain of weight. Thus, body mass at departure varied, being larger in birds after some days of refuelling. The decision to depart immediately or to stay and gain body mass must be taken individually according to information gathered from the environment. Weather conditions might be an additional factor which strongly influences the stopover time (Alerstam 1979, Weber & Hedenström 2000). However, in the period of Knot autumn migration, weather conditions along the southern Baltic coast are usually favourable for birds flying in western direction and there are only few days with strong head winds at low altitudes making westward flight impossible (Remisiewicz 1996).

Adults and juveniles that stop at the non-tidal areas of the southern Baltic were recorded later in tidal areas of Western Europe (Gromadzka 1992), and the recovery rate of Knots ringed in the Puck Bay is higher than in many other wader species (Meissner & Remisiewicz 1998). Thus, it seems that Knots cope with poor feeding conditions at a low quality stopover site, yet accumulate sufficient energetic reserves for further migration. It is possible that the lack of additional energetic costs related to a large gizzard is one of the reasons of the high refuelling rate in Knots feeding on low quality food on the southern Baltic sandy coasts. Despite of a longer period of stay, juveniles seemed to search for better feeding places less often than adults. One of the reasons might be that juveniles lack previous experience considering high profits of foraging on molluscs and about the relative richness of tidal mudflats of the Wadden Sea.

REFERENCES

Alerstam T. 1979. Wind as selective agent in bird migration. Ornis Scand. 10: 76–93.

Battley P.F. & Piersma T. 2005. Adaptive interplay between feeding ecology and features of the digestive tract in birds. In: Starck J.M. & Wang T. (eds) Physiological and ecological adaptations to feeding in vertebrates: 201–227. Science Publ., Enfield.

Busse P. 1982. Finding of local passage direction as the result of an analysis of retraps and short distance direct-recoveries. Not. Orn. 22: 31–39. (in Polish with English summary).

Brewka B., Meissner W., Sikora A. & Skakuj M. 1987. Four years of the activity of Waterbird Research Group "KULING". Ring 11: 339–347.

Dekinga A., Dietz M.W., Koolhaas A. & Piersma T. 2001. Time, course and reversibility of changes in the gizzards of red knots alternately eating hard and soft food. J. Exp. Biol. 202: 2831–2837.

Dierschke V. 1995. Der Knutt *Calidris canutus*. Ber. Vogelw. Hiddensee 12: 129–132.

Dierschke V. & Rippe H. 1997. Ernährungsbedingungen für Kiebitzregenpfeifer *Pluvialis squatarola* und Knutts *Calidris canutus* im Windwatt bei Hiddensee, deutsche Ostseeküste. Vogelwelt 118: 269–275.

Górecki D. 2003. Behaviour of the Curlew Sandpiper *Calidris ferruginea* (Ponn. 1763) during autumn migration in the Gulf of Gdańsk. PhD thesis. Warmia and Masuria University, Olsztyn. (in Polish)

Gromadzka J. 1992. Knots on the Polish Baltic coast. Wader Study Group Bull. 64 Suppl.: 161–166.

Gromadzka J. 1998. Wader ringing at the Vistula mouth (Baltic coast, Poland) – a summary of the long-term studies. Ring 20: 5–20.

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

Kautsky L. 1998. Monitoring eutrophication and pollution in estuarine environments – focusing on the use of benthic communities. Pure Appl. Chem. 70: 2313–2318.

Kube J. 1994. Aspekte der Nahrungsökologie ziehender Limikolen an der südlichen Ostseeküste. Corax 15, Sonderheft 2: 57–72.

Meissner W. 1992. Knots' autumn migration in the western part of the Gulf of Gdańsk, Poland: preliminary results. Wader Study Group Bull. 64 Suppl.: 167–171.

Meissner W. 1998. Some notes on using walk-in traps. Wader Study Group Bull. 86: 33–35.

Meissner W. 2000. The wader station. In: Busse P. (ed) Bird Station Manual: 98–102. University of Gdańsk, Gdańsk.

Meissner W. 2005a. Variation in timing of the Siberian Knot *Calidris c. canutus* autumn migration in the Puck Bay region (southern Baltic). Acta Ornithol. 40: 95–101.

Meissner W. 2005b. Autumn migration of the Broad-billed Sandpiper *Limicola falcinellus* on the southern Baltic Coast. Ring. Migrat. 22: 171–176.

Meissner W. & Górecki D. 2006. Biometrics and body mass variation of Curlew Sandpiper *Calidris ferruginea* caught on the Puck Bay coast, Poland, during southward migration. Internat. Wader Studies 19: 125–129.

Meissner W. & Kamont P. 2005. Seasonal changes in body size and mass of Red Knots *Calidris canutus* during autumn migration through southern Baltic. Ornis Svecica 15: 97–104.

Meissner W. & Koziróg L. 2001. Biometrics of Turnstone *Arenaria interpres* migrating in autumn through Gulf of Gdańsk region. Ornis Svecica 11: 181–188.

Meissner W. & Sikora A. 1995. Spring and autumn migration of waders (Charadrii) on the Hel Peninsula. Not. Orn. 36: 205–239. (In Polish with English summary)

Meissner W. & Ściborski M. 2002. Autumn migration of the Bar-tailed Godwit (*Limosa lapponica*) in the Gulf of Gdańsk region. Ring 24: 3–15.

Nebel S., Piersma T., van Gils J., Dekinga A. & Spaans B. 2000. Length of stopover, fuel storage and sex-bias in the occurrence of Red Knots *Calidris c. canutus* and *C. c. islandica* in the Wadden Sea during southward migration. Ardea 88: 165–176.

Pehrsson O. 1987. Effects of body condition on molting in Mallards. Condor 89: 329–339.

Pienkowski M.W. & Minton C.D.T. 1973. Wing length changes of the Knot with age and time Since Mount. Bird Study 20: 63–68.

Piersma T., Davidson N.1992. The migrations and annual cycles of five subspecies of Knots in perspective. Wader Study Group Bull. 64 Suppl.: 187–197.

Piersma T., Dekinga A., van Gils J.A., Achterkamp B. & Visser G.H. 2003. Cost-benefit analysis of mollusc-eating in a shorebird. I. Foraging and processing costs estimated by the doubly labeled water method. J. Exp. Biol. 206: 3361–3368.

Piersma T., Hoekstra R., Dekinga A., Koolhaas A., Wolf P., Battley P. & Wiersma P. 1993. Scale and intensity of intertidal habitat use by Knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. Neth. J. Sea Res. 31: 331–357.

Piersma T., Prokosch P. & Bredin D. 1992. The migration system of Afro-Siberian Knots *Calidris canutus canutus*. Wader Study Group Bull. 64 Suppl.: 52–63.

Prater A.J., Marchant J.H. & Vuorinen J. 1977. Guide to the identification and ageing of Holarctic waders. BTO, Tring.

Remisiewicz M. 1996. Influence of weather conditions on the autumn migration of Dunlin (*Calidris alpina*) at the southern Baltic. Ring 18: 73–88.

Schaub M., Pradel R., Jenni L. & Lebreton J.-D. 2001. Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. Ecology 82: 852–859.

StatSoft Inc. 2001. STATISTICA (data analysis software system), version 6. www.statsoft.com.

Stawarczyk T. 1984. Aggression and its suppression in mixed-species wader flocks. Ornis Scand. 15: 23–57.

van Gils J.A., Battley P.F., Piersma T. & Drent R. 2005. Reinterpretation of gizzard sizes of red knots worldwide emphasis overriding importance of prey quality at migratory stopover sites. Proc. R. Soc. Lond. B. 272: 2609–2618.

van Gils J.A., Piersma T., Dekinga A. & Dietz M.W. 2003. Cost-benefit analysis of mollusc-eating in a shorebird. II. Optimizing gizzard size in the face of seasonal demands. J. Exp. Biol. 206: 3369–3380.

Weber T. P. & Hedenström A. 2000. Optimal stopover decisions under wind influence: the effects of correlated winds. J. Theor. Biol. 205: 95–104.

Włodarczak-Komosińska A. 2004. Feeding ecology of Dunlin *Calidris alpina* (L. 1758) and Little Stint *Calidris minuta* (Leisler 1822) during autumn migration in the Gulf of Gdańsk. PhD thesis. Warmia and Masuria University. Olsztyn. (In Polish)

Zar J.H. 1996. Biostatistical analysis. Third edition. Prentice-Hall, London.

SAMENVATTING

Voor Kanoeten *Calidris c. canutus* op najaarstrek lijkt het zuiden van de Oostzee op het eerste gezicht een matig tussenstopgebied. De zandige kust herbergt amper schelpdieren en de voedselomstandigheden zijn onvoorspelbaar vanwege de windrichting en windkracht, die de waterstand en daarmee de mogelijkheid om voedsel te zoeken bepalen. Om te onderzoeken of deze onvoorspelbare voedselomstandigheden een weerslag hebben op de snelheid waarmee Kanoeten lichaamsreserves aanleggen, werden vogels gevangen en gewogen in de Puck Baai in Polen. In dit gebied aten Kanoeten vooral Zeeduizendpoot *Nereis* sp., Vlokreeft *Gammarus* sp., Wadslakje *Hydrobia* sp. en kleine insecten die ze van het zand oppikten. Er werden aanzienlijk meer jonge (1071) dan oude vogels (410) gevangen. Op basis van terugvangsten in hetzelfde seizoen werd geschat dat de verblijfsduur van jonge vogels 9,4 dagen bedroeg, van oude vogels slechts 3,0 dagen. Het kwam als een verrassing dat de gewichtstoename per dag (adulte vogels 2,4 g, jonge vogels 2,7 g) vergelijkbaar was met de toename in de Nederlandse Waddenzee en de Oostzeekust van ZO-Zweden. Er wordt verondersteld dat het lage voedselaanbod gecompenseerd wordt door het ontbreken van getij waardoor de vogels permanent kunnen eten. Ook zou het ontbreken van de noodzaak de maag te vergroten, zoals schelpeters dat doen, een extra energetisch voordeel kunnen opleveren.   (JP)