

Body Condition and Fuel Deposition Patterns of Calidrid Sandpipers During Migratory Stopover

Authors: Choi, Chiyeung, Gan, Xiaojing, Ma, Qiang, Zhang, Kejia,

Chen, Jiakuan, et al.

Source: Ardea, 97(1): 61-70

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.097.0108

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Body condition and fuel deposition patterns of calidrid sandpipers during migratory stopover

Chiyeung Choi¹, Xiaojing Gan¹, Qiang Ma², Kejia Zhang², Jiakuan Chen¹ & Zhijun Ma^{1,*}

Choi C.Y., Gan X.J., Ma Q., Zhang K.J., Chen J.K. & Ma Z.J. 2009. Body condition and fuel deposition patterns of calidrid sandpipers during migratory stopover. Ardea 97(1): 61–70.

We compared seasonal variations in body condition and fuel deposition patterns of five calidrid sandpipers at Chongming Dongtan (eastern China), a stopover site in the East Asian-Australasian Flyway. We tested the hypothesis that long-distance migrants show different body condition and fuel deposition patterns relative to those undertaking short-distance flights. Results indicated that the body condition and fuel deposition patterns of the sandpipers varied between the northward and southward migration seasons and between ageclasses. Great Knots Calidris tenuirostris and Red Knots Calidris canutus migrate southwards on a long-distance nonstop flight from Chongming Dongtan to northwest Australia, while covering on the return flight a relatively short-distance between Chongming Dongtan and the north Yellow Sea region. Both species attained a significantly higher body condition at Chongming Dongtan during the southward than northward migration. Moreover, they showed a significant increase in body condition at Chongming Dongtan during northward migration stopover, which we see as a recovery from the long flight from Australia. In contrast, Red-necked Stints Calidris ruficollis and Long-toed Stints Calidris subminuta, employing series of relatively short-distance flights during migration, indicated no significant difference in departure body condition at Chongming Dongtan between seasons, nor significant increase in body condition during either migration stopover. Dunlins Calidris alpina on the other hand, showed a significantly higher body condition during northward than southward migration stopover, most likely in anticipation of the longer travelling distance after leaving Chongming Dongtan during northward migration. This study confirms that the body condition and fuel deposition patterns among shorebird species that undertake long-distance nonstop flights are different from those that undertake series of short-distance flights, suggesting that the comparison of body condition and fuel deposition patterns of calidrid sandpipers can be an important tool to understand their migration strategies.

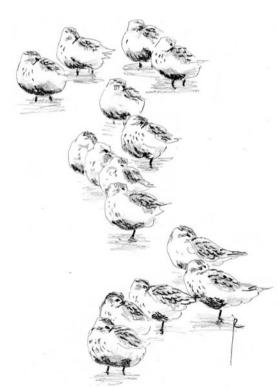
Key words: migration strategy, fuel deposition, body condition, calidrid sandpipers, East Asian-Australasian Flyway

¹Coastal Ecosystems Research Station of the Yangtze River Estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, 220 Handan Road, Shanghai, 200433, P.R. China; ²Chongming Dongtan National Nature Reserve, Chongming, 202183, P.R. China; *corresponding author (zhijunm@fudan.edu.cn)



The fuel deposition rate of migrants at stopover sites may reflect their migration strategies (Harrington *et al.* 1991, Scheiffarth *et al.* 2002, Lindström 2003). Piersma (1987) categorised the migration strategies of Afro-

European shorebirds into three major travel schemes: 'hop', 'skip' and 'jump'. These in turn were then renamed as short, intermediate and long distance bouts to describe the migration strategies used by North American shorebirds (O'Reilly & Wingfield 1995). The fuel deposition rate at stopover sites was one of the



crucial factors determining the overall speed of migration and its success (Schaub & Jenni 2000b). Its variation determines the stopover duration and the length of each flight bout between stopover sites (Schaub & Jenni 2001a,b).

Factors as sex, age or moult, as well as variation in season, weather, or geography may have an impact on the migration strategies employed. This can lead to different migration strategies among populations of the same species, e.g. Ruddy Turnstone Arenaria interpres (Nettleship 2000) and Bar-tailed Godwit Limosa lapponica (Scheiffarth et al. 2002), or among seasons within the same population, e.g. Semipalmated Sandpiper Calidris pusilla (Gratto-Trevor 1992) and Red Knot Calidris canutus (Helseth et al. 2005). Similarly, age-classes may differ in migration strategy as in Honey Buzzard Pernis apivorus (Hake et al. 2003), Dunlin Calidris alpina (Gromadzka 1989) and Great Knot Calidris tenuirostris (Battley 2002). Moreover, migration strategies may change through the migratory season. For example, arctic juvenile waders started migration with short hops before flying long bouts to the wintering grounds (Lindström et al. 2002), and adult White-rumped Sandpipers Calidris fuscicollis made a long-distance non-stop flight over the Atlantic Ocean before gradually 'hopping' to the wintering ground in South America (Harrington et al. 1991). In general, body condition at stopover sites varied with the distance of the next flight (Harrington et al. 1991, Scheiffarth et al. 2002, Lindström et al. 2002). Therefore, we expect that birds about to take a long-distance nonstop flight have more energy reserves than those taking a short-distance flight.

Supporting five million migratory shorebirds, the East Asian-Australasian Flyway is a major component of the Global Flyway (Barter 2002, Piersma 2007). Previous research along the East Asian-Australasian Flyway has yielded important insights into the variation in migration strategies of different shorebirds (Battley et al. 2000, 2005, Driscoll & Mutsuyuki 2002, Gill et al. 2005). Based on satellite tracking, recovery records and flight range estimates, these studies have shown that shorebirds are capable of a nonstop transoceanic flight between Australia and East China. Moreover, Tulp et al. (1994) suggested that large calidrid sandpipers such as Great Knot and Red Knot, fly directly from northwest Australia to the east China coast, while small species such as Red-necked Stint Calidris ruficollis are bound to stage and refuel in southeast Asia before continuing their northward migration. Their hypotheses are supported by the observation of Red-necked Stints in large flocks in southeast Asia



Figure 1. Map of Chongming Dongtan in the Yellow Sea region. The inset shows the location of Yellow Sea region within the East Asian–Australasian Flyway.

during migration, while Great Knots and Red Knots occurred only in small numbers (Bamford *et al.* 2008). However, the relationship between energy deposition patterns at stopover sites and migration strategies has not been studied in detail in the East Asian–Australasian Flyway.

Chongming Dongtan (hereafter CMDT), China, is located in the middle of the East Asian-Australasian Flyway (Fig. 1) and is an important stopover site for shorebirds (Ma et al. 2004). Calidrid sandpipers at CMDT account for more than 70% of all shorebirds counted (Jing et al. 2007). Of the calidrid species, Great Knot, Red Knot and Red-necked Stint winter mainly in Australia although some Red-necked Stints winter in the Philippines and Malaysia and small numbers of Great Knots winter in southeast Asia (Bamford et al. 2008). Most of the Long-toed Stints Calidris subminuta winter in southeast Asia and the Philippines, with a few hundred in Australia, while Dunlins winter mainly in East Asia including CMDT (Hayman et al. 1986, Piersma et al. 1996). Bamford et al. (2008) indicated that in boreal autumn no staging site supports more than 0.25% of the estimated flyway population

beyond CMDT along the coast of southeast China including Taiwan. This suggests that sandpipers are likely to fly to southeast Asia or even directly to Australia after leaving CMDT during southward migration. In contrast, in boreal spring several staging sites supporting more than 1% of the estimated population of the flyway have been identified in the nearby Yellow Sea region (Bamford *et al.* 2008), north of CMDT. This indicates that sandpipers can travel for a relatively short distance before making another stopover after leaving CMDT during northward migration (Barter *et al.* 1997). Due to the diverse role of CMDT as stopover site, there is reason to expect differences in body condition and fuel deposition patterns among species and between spring and autumn.

In this study, we compare the body condition and fuel deposition patterns of five calidrid species (Great Knot, Red Knot, Red-necked Stint, Long-toed Stint and Dunlin) at CMDT during northward and southward migration. Moreover, we relate the energetic dynamics to the migration strategies of each of the species by testing the hypothesis that species undertaking long-distance nonstop flights show different body condition and fuel deposition patterns relative to those undertaking a short-distance flight.

METHODS

Study site

CMDT (31°30'N, 122°05'E) is located on the eastern side of Chongming Island in the Yangtze River estuary. It is an estuarine wetland, consisting of salt marshes and bare tidal flats with an estimated area of 102 km² available for shorebirds (Jing et al. 2007). The dominant plant species of the salt marshes includes the native Common Reed Phragmites australis, Sea Bulrush Scirpus mariqueter, and introduced Smooth Cordgrass Spartina alterniflora. CMDT supports as many as 250 000 shorebirds annually (Barter 2002). It has been recognised as a Ramsar site and listed as one of BirdLife's 'Important Bird Areas'. Calidrid sandpipers forage mainly at the Scirpus zone and on the bare tidal flats, where the highest density of prey for shorebirds occur (Jing 2005). The prey for shorebirds include infaunal macrobenthos, consisting mainly of bivalves, dominating the bare flats, and epifaunal macrobenthos, consisting mainly of crustaceans and gastropods, dominating the salt marshes (Jing et al. 2007). Of the five species of calidrid sandpipers in this study, Dunlin winters at CMDT, while the other four species only stage at CMDT during migration.

Bird capture and measurement

Shorebirds were captured and ringed at CMDT during migratory stopovers each year from 2003 to 2007. Catching periods were between 8 March and 22 May and between 23 July and 19 October. The capture efforts varied between years with a minimum of 14 (in 2003) and a maximum of 59 days (in 2007) during northward migration, and a minimum of 17 (in 2004) and a maximum of 78 days (in 2007) during southward migration. Local hunters, using clap nets (2.5 x 12 m), decoys and mimicked bird calls, were hired for the catch, which took place in the mudflats. All birds captured were provided with numbered metal rings issued by the National Bird Banding Centre of China and coloured leg flags on tibia or tarsus. Wing length was measured as flattened and stretched wing chord with a stopped ruler to the nearest 1 mm (maximum chord), bill length (exposed culmen) and tarsus were measured with callipers to the nearest 0.1 mm. Body mass was measured to the nearest 0.1 g using electronic digital balances. Most captured birds were processed and released within 3-4 hours.

In late boreal summer and autumn, birds were aged as either adults, second-year or first-year (calendar year) birds, based mainly on the wear of primaries, since adults have more worn primaries than first-year birds, and second-year birds have a distinct moult pattern in most calidrid species (Prater et al. 1977). The same ageing method was used in boreal spring except that adults have fresh primaries while second-year birds have either worn primaries or partially moulted primaries (Prater et al. 1977). The Dunlin is an exception as most adults moult their flight-feathers completely before the southward migration, resulting in fresh wing and tail feathers as first-year birds have. Adult Dunlin were therefore distinguished by a combination of criteria, including the remnants of breeding plumage on belly, the pattern of white bars on primary coverts (Persson 2007) and the colour of inner median coverts (Gromadzka 1986).

Data analysis

Data of each calidrid species were classified into three groups: adults on northward migration, adults on southward migration and first-year birds on southward migration. In northward migration, only adults were analyzed since second-year calidrid sandpipers generally do not attempt breeding in their first summer and rarely were recorded at CMDT. The Dunlin was an exception, but since first-year Dunlins also attempt breeding (Holmes 1966; Pienkowski *et al.* 1979, Warnock & Gill 1996), we have pooled all Dunlins and treated

them as adults. In southward migration, second-year birds were excluded from further analysis because their numbers were negligible (<3% of total numbers for each species).

Groups with fewer than 20 records in any season were excluded from analysis, included here are adult Great Knots and Red Knots on southward migration. Individuals were excluded if they were injured or dead, were weighed more than five hours after capture, had wet feathers, or could not be aged with certainty, as well if they had been caught earlier in the same season. This resulted in a dataset of 6412 Great Knot, 642 Red Knot, 895 Red-necked Stint, 1631 Long-toed Stint and 1606 Dunlin for analysis. Sample sizes may differ among analyses due to incomplete ringing records.

The condition index (hereafter CI), provides a nondestructive method to estimate individual energy stores by correcting body mass for body size (Schulte-Hostedde et al. 2005). CI was calculated as (body mass / body size variable) x 100 (Winker et al. 1992, Winker 1995). Although the wing length is commonly used as correcting factor for structural size in shorebirds (Castro & Myers 1990), it varies with age, sex and season in the five study species (Appendix 1), thus giving a biased result. For example, the primaries of Great Knots are more worn (shorter) during southward than northward migration because they moult their primaries on the wintering grounds (Prater et al. 1977). Therefore, bill length or tarsus length were preferred as body size variables in several studies (Mascher & Marcstrom 1976, Shepherd et al. 2001, Dinsmore & Collazo 2003). Regression of wing length on bill and tarsus length indicated that there was always a stronger correlation between bill length and wing length than between tarsus length and wing length (Appendix 2). Therefore, we used bill length as body size variable to calculate CI.

Data from all years were pooled for further analysis

for two reasons. First, because we focused on seasonal variation in body condition, and secondly because annual differences in CI among species were inconsistent. One-way ANOVAs were used to compare the CI by season and age-class for each species separately. Some of the data did not qualify for the assumptions regarding the homogeneity of variances nor were they normally distributed, but these deficiencies can be neglected due to the large sample sizes (Zar 1999).

In each season we designated the earliest captured 20 and the latest captured 20 individuals of each species as those just arrived and those just about to depart, respectively. Most of these records come from the years 2005–2007, when coverage was most complete. The two groups were compared by one-way ANOVA to test if CI differed among arriving and departing individuals. To avoid biases, groups containing less than 60 individuals were excluded in this analysis. In addition, linear regression of CI on capture date (Julian date) was performed to assess changes of CI with time. Due to small sample sizes, recapture data were not used to calculate fuel deposition patterns.

All analyses were performed using SPSS 12.0 for Windows (SPSS Inc. 2003). Significance level (α) 0.05 was used for all statistical tests if not otherwise mentioned, and statistics are stated as mean \pm SD.

RESULTS

Body condition

CI of first-year Great Knots and Red Knots on southward migration were significantly higher than the CI of adults on northward migration (Table 1). Similarly, adult Rednecked Stints and Long-toed Stints showed significantly higher CI on southward than on northward migration. Dunlins showed a reverse pattern, with CI on northward

Table 1. Comparison of the Condition Index CI among season/age-classes in five sandpiper species (data from 2003–2007). Adult Great Knots and Red Knots during northward migration were not included because of small sample sizes. Different superscript letters indicate significant differences among classes (Tukey HSD multiple comparison tests, P < 0.05). Given are means \pm SD, and sample sizes in parentheses.

Species	Southward migration		Northward migration	F	P
	First-year birds	Adults			
Great Knot	368 ± 50.6^{a} (240)	-	301 ± 31.3 ^b (4856)	965.3	< 0.001
Red Knot	$333 \pm 48.9^{a} (54)$	-	$302 \pm 36.2^{b} (579)$	33.8	< 0.001
Red-necked Stint	145 ± 23.3^{a} (222)	$161 \pm 25.4^{b} (119)$	$150 \pm 15.3^{\circ} (544)$	27.9	< 0.001
Long-toed Stint	131 ± 15.7^{a} (1308)	$153 \pm 23.5^{b} (280)$	140 ± 14.5^{a} (22)	179.3	< 0.001
Dunlin	130 ± 11.9^{a} (456)	$138 \pm 14.7^{b} (73)$	$153 \pm 17.5^{\circ} (917)$	344.2	< 0.001

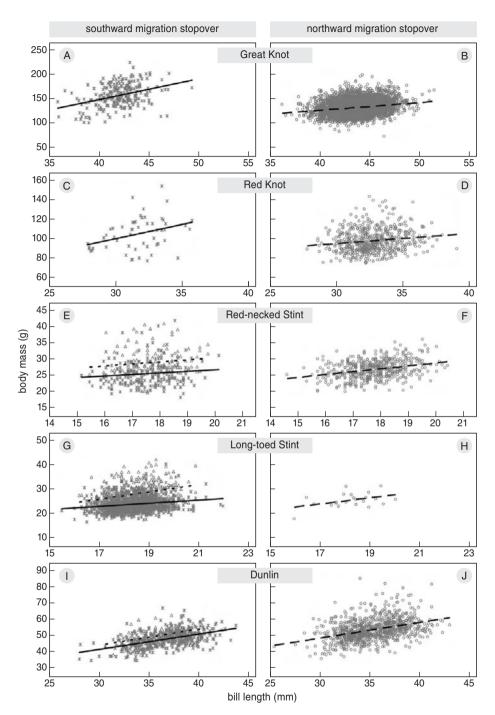


Figure 2. Body mass plotted against bill length during southward (left) and northward (right) migration stopover. The stars denote first-year birds during southward migration stopover; triangles denote adults during southward migration stopover; circles denote all individuals during northward migration stopover; solid lines denote the trend for first-year birds during southward migration stopover; dotted lines denote the trend for adults during southward migration stopover; long dashed lines denote the trend for all individuals during northward migration stopover.

migration significantly higher than on southward migration. Moreover, in species where both adults and firstyear birds were present during southward migration (Red-necked Stints, Long-toed Stints and Dunlins), the CI of adults was always significantly higher than that of first-year birds (Table 1, Fig. 2).

When comparing the CI of the earliest and latest 20 captured Great Knots on southward and northward migration, significantly higher values occurred during southward migration (Table 2). Other species showed similar patterns. However, the CI of the latest 20 captured Red-necked Stints did not differ significantly among seasons and age-classes. In addition, the CI of the latest 20 captured adult and first-year Long-toed Stints did not differ significantly during southward migration. There were no significant differences in CI between first-year and adult Dunlins on southward migra-

tion. In both the earliest and latest 20 individuals adults on northward migration had a higher CI than birds on southward migration (Table 2).

Fuel deposition rates

Linear regression of CI on capture date of adults during southward migration showed that there was no significant change in CI in Great Knots, Red Knots and Rednecked Stints, a decrease in Long-toed Stints, and an increase in Dunlins (Table 3). First-year birds of all species showed a significant increase in CI during southward

Table 2. Comparison of the Condition Index CI of the earliest 20 and latest 20 captured sandpipers between seasons and age-classes (data from 2003–2007). Categories with a total sample size of fewer than 60 were excluded. Different superscript letters indicate significant differences among classes (Tukey HSD multiple comparison tests, P < 0.05). Given are means \pm SD. S: southward migration, N: northward migration.

Species	Season/age-classes	Earliest 20 individuals			Latest 20 individuals			
		CI	F	P	CI	F	P	
Great Knot	First-year birds (S) Adults (N)	339 ± 33.0 307 ± 27.7	11.4	0.002	377 ± 59.5 324 ± 46.3	9.69	0.004	
Red-necked Stint	First-year birds (S) Adults (S) Adults (N)	143 ± 20.7^{a} 164 ± 26.9^{b} $153 \pm 9.2^{a,b}$	5.29	0.008	160 ± 29.2 158 ± 31.7 158 ± 12.8	0.032	0.968	
Long-toed Stint	First-year birds (S) Adults (S)	129 ± 11.8^{a} 177 ± 22.9^{b}	69.5	< 0.001	134 ± 24.1 148 ± 24.0	3.22	0.081	
Dunlin	First-year birds (S) Adults (S) Adults (N)	126 ± 11.8^{a} 130 ± 12.3^{a} 148 ± 12.9^{b}	18.7	<0.001	133 ± 10.1^{a} 141 ± 10.7^{a} 189 ± 25.3^{b}	65.8	<0.001	

Table 3. Summary of linear regressions of Condition Index (Y) with date (X, 1 = 1 January). Equations are $Y = m \times X + c$. S: southward migration, N: northward migration.

Species	Season/age	n	m	с	R^2	F	P
Great Knot	First-year birds (S)	240	1.36	12.2	0.13	36.3	<0.001
	Adults (N)	4856	0.324	270	0.01	31.8	< 0.001
Red Knot	First-year birds (S)	53	1.67	-91.2	0.09	5.54	0.027
	Adults (N)	579	0.428	254	0.03	17.7	< 0.001
Red-necked Stint	First-year birds (S)	222	0.517	13.9	0.07	16.6	< 0.001
	Adults (S)	119	-0.134	190	0.01	0.32	0.577
	Adults (N)	544	-0.014	151	0.01	0.06	0.815
Long-toed Stint	First-year birds (S)	1308	0.111	106.7	0.01	7.09	0.008
	Adults (S)	279	-0.533	270	0.03	8.25	0.004
	Adults (N)	22	0.694	52.7	0.06	1.26	0.275
Dunlin	First-year birds (S)	456	0.332	41.5	0.10	52.1	< 0.001
	Adults (S)	73	0.276	64.8	0.12	9.58	0.003
	Adults (N)	917	0.214	134	0.04	35.2	< 0.001

migration. During northward migration, adult Great Knots, Red Knots and Dunlins showed a significant increase in CI, while changes were non-significant in Rednecked Stints and Long-toed Stints (Table 3).

DISCUSSION

Our study provided evidence that body condition and fuel deposition patterns vary between the migration seasons and between age-classes. Moreover, we showed that Great Knot and Red Knot, which undertake a nonstop trans-oceanic flight, attained significantly higher body condition at CMDT during their southward than northward migration. These species also increased most in body condition after a long-distance flight from Australia during northward migration. In contrast, Rednecked Stints and Long-toed Stints, which undertake a series of relatively short-distance flights, showed neither a difference in departure body condition between seasons, nor - at least in adults - a significant increase in body condition during stopover at CMDT. Moreover, first-year birds of species of which both age-classes were present at CMDT in autumn, showed a significant increase in body condition, but not the adults, with Dunlin as an exception. This study confirms that the body condition and fuel deposition patterns of shorebird species undertaking long-distance nonstop flights are different from those undertaking a series of shortdistance flights.

Body condition

Previous studies concluded that most Great Knots and Red Knots make a long-distance direct flight between Australian wintering grounds and mainland China stopover areas, but may make short distance hops when moving along the stopover sites between southern and northern Yellow Sea region (Tulp et al. 1994, Barter et al. 1997, Battley et al. 2000, Battley 2002, Battley et al. 2005). Wilson & Barter (1998) have speculated that the northern Yellow Sea region may be a final staging area for Great Knots before reaching their breeding grounds. Such speculation is further supported by the records of CMDT-flagged Great Knots and Red Knots in Bohai Bay (Fig. 1) within a month after being ringed at CMDT (X. Hui, pers. comm.). In this study, the low body condition of Great Knots and Red Knots at arrival at CMDT on northward migration is the likely result of depleted energy stores after a long flight. When going south, the preparation for the same longdistance flight is a plausible explanation for their high body condition at CMDT. The lower fuel loads for northward migration may be explained by relatively short travel bouts ahead.

Although the overall body conditions of adult Rednecked Stints and Long-toed Stints were significantly higher in southward than northward migration stopover, neither species showed significant differences in body condition prior to departure between different seasons and age-classes, suggesting that they might fly for similar distances in both seasons after leaving CMDT. These observations are consistent with recoveries of ringed Red-necked Stint (Tulp et al. 1994) and records of Long-toed Stints in large flocks in northern and southern Yellow Sea regions and also in southeast Asia (Bamford et al. 2008), which suggest that they take a relatively short distance flight after leaving CMDT on southward and northward migration. Moreover, we found that part of the adult Long-toed Stints were in active primary moult (C. Choi, unpubl. data), which is an energy-consuming process, possibly resulting in the observed decrease in body condition over time.

Our results indicated that the body condition of Dunlins during northward migration was significantly higher than during southward migration, irrespective of the overall, arrival or departure body condition. Recent study indicated that large numbers of Dunlins overwinter in southeast China including CMDT (Barter et al. 2006). Thus the Dunlins captured at CMDT during southward migration were either winterers at CMDT or close to their wintering grounds in southeast China. Individuals at wintering grounds generally carry low levels of fat (Winker 1995), which may give them better manoeuvrability when escaping from predators (Zwarts et al. 1990, Swanson et al. 1999). Dunlins at CMDT were in higher body condition during northward than southward migration. On northward migration, energy is needed for migratory flight and is acting as extra reserves enabling the birds to face poor weather conditions in the north (O'Reilly & Wingfield 1995).

On southward migration, most of the captured Great Knots and Red Knots were first-year birds. This indicates a differential use of stopover sites and different migration strategies used by different age-classes. The few records of adult Great Knots support Battley's speculation (2002) that adults may fly directly from the Sea of Okhotsk to Australia, without stopping in east and southeast Asia. This indicates that migration strategies can vary between age-classes.

Fuel deposition patterns

Our results indicated that fuel deposition patterns varied among species and age-classes during migration stopovers. During southward migration, first-year Red-

necked Stints and Long-toed Stints had low body condition on their initial arrival at CMDT, and exhibited a significant increase of body condition during stopover. Contrarily, the initial arriving adults had high body condition, and showed no significant increase in body condition during stopover. We suspect that the adults had deposited large amounts of energy in the north Yellow Sea region before arriving at CMDT and they may also be effective fliers spending relatively less amount of energy during migration flight than first-year birds, which are inexperienced on migratory flights and more energetically constrained than adults (Rimmer & McFarland 2000). A similar difference in deposition of body stores among age classes was reported in Red Knots at Ottenby in Sweden (Helseth et al. 2005). First-year Great Knots and Red Knots showed a significant increase in body condition at CMDT during southward migration stopover as well. This suggests that CMDT is an important stopover site for first-year birds. The significant increase in body condition in both adult and first-year Dunlins on southward migration may act as an insurance against food shortages after arriving at the wintering grounds (Johnson 1985).

On northward migration stopover, Great Knots and Red Knots showed a significant increase in body condition at CMDT, which can be a response to heavy fuel loss during the trans-oceanic flight from Australia. No significant change in body condition was found in Rednecked Stints and Long-toed Stints at CMDT. These birds are likely to take a short-distance flight before arriving and after departing CMDT, which does not necessitate as much replenishment as in migrants using long-distance nonstop flights (Piersma 1987). The increase in body condition of Dunlins at CMDT on northward migration is likely to be a preparation for migratory flight because they overwinter at CMDT and in the surrounding regions.

Conservation implications

Identification of important staging sites for shorebirds according to their numerical distribution (Bamford *et al.* 2008) is the first step for making pertinent management decisions. Once these areas are known, it is important to assess their importance based on their function as topping-up or moulting site. At CMDT, first-year birds of the five calidrid species showed significant increases in body condition during southward migration. This suggests that CMDT is especially important for the energy deposition of first-year birds during southward migration, although the number of shorebirds is much lower during southward than northward migration stopover (Ma *et al.* 2002).

Our results provide insight into the importance of stopover sites further north of CMDT. The relatively low departure body condition of Great Knots and Red Knots during their stopover on northward migration do not seem to be adequate for another long-distance flight. Thus, they must continue to refuel outside CMDT before arriving at the breeding grounds. Adult Red-necked Stints and Long-toed Stints, which stopover at CMDT during southward migration, exhibited no significant changes in body stores which suggests that they may have gained enough energy at stopover sites further to the north before arriving at CMDT. Additional studies are needed in the Yellow Sea region to understand how different stopover sites are used by the various sandpiper species. Management efforts for shorebird conservation thus need to have a regional perspective along the East Asian-Australasian Flyway.

ACKNOWLEDGEMENTS

This study was financially supported by the National Basic Research Program of China (Grant no. 2006CB403305), National Natural Science Foundation of China (Grant no. 30670269, 30400057) and Shanghai Scientific and Technology Foundation (07DZ12038). We thank the Chongming Dongtan National Nature reserve for facilitating our fieldwork as well as all the staffs and volunteers involved in the bird banding work, which included Xiao Yuan, Hongxi Zang, Si Zheng, Ning Hua, Xin Hui, Yinting Cai, Zhongquan Zhang and Weiguo Jin. We would also like to thank Christer Persson, Yong Wang, Julia Stahl, Jouke Prop and two anonymous referees for their comments on earlier versions.

REFERENCES

Bamford M., Watkins D., Bancroft W. & Tischler G. 2008. Migratory shorebirds of the East Asian-Australasian Flyway. Wetlands International Oceania.

Barter M. 2002. Shorebirds of the Yellow Sea: importance, threats and conservation status. Wetlands International Global Series 9, International Wader Studies 12, Canberra, Australia.

Barter M., Lei G., Cao L., Gu C. M., Hu H.X., Ji W.T., Jiang Y., Ma Z.J. & Wang H. 2006. Waterbird survey of the middle and lower Yangtze River Floodplain (February 2005). China Forestry Publishing House.

Barter M., Tonkinson D., Sixian T., Xiao Y. & Fawen Q. 1997. Staging of Great Knot *Calidris tenuirostris*, Red Knot *C. canutus* and Bar-tailed Godwit *Limosa lapponica* at Chongming Dao, Shanghai: jumpers to hoppers? Stilt 31: 2–11.

Battley P.F. 2002. Behavioural ecophysiology of migrating Great Knots. PhD thesis, Griffith University, Brisbane, Australia.

Battley P.F., Piersma T., Dietz M.W., Tang S., Dekinga A. & Hulsman K. 2000. Empirical evidence for differential organ reductions during trans-oceanic bird flight. Proc. R. Soc. Lond. B 267: 191–195.

- Battley P.F., Rogers D.I., van Gils J.A., Piersma T., Hassell C.J., Boyle A. & Yang H.Y. 2005. How do Red Knots *Calidris canutus* leave Northwest Australia in May and reach the breeding grounds in June? Predictions of stopover times, fuelling rates and prey quality in the Yellow Sea. J. Avian Biol. 36: 494–500.
- Castro G. & Myers J.P. 1990. Validity of predictive equations for total body fat in sanderlings from different nonbreeding areas. Condor 92: 205–209.
- Dinsmore S. J. & Collazo J.A. 2003. The influence of body condition on local apparent survival of spring migrant sanderlings in coastal North Carolina. Condor 105: 465–473.
- Driscoll P.V. & Mutsuyuki U. 2002. The migration route and behaviour of Eastern Curlews *Numenius madagascariensis*. Ibis 144: E119–E130.
- Gill R.E.J., Piersma T., Hufford G., Servranckx R. & Riegen A. 2005. Crossing the ultimate ecological barrier: evidence for an 11 000-km-long nonstop flight from Alaska to New Zealand and eastern Australia by Bar-tailed Godwits. Condor 107: 1–20.
- Gratto-Trevor C.L. 1992. Semipalmated Sandpiper (Calidris pusilla). In: Poole P. & Gill F. (eds) The Birds of North America, no. 6. Academy of Natural Sciences, Philadelphia, and AOU, Washington, D.C.
- Gromadzka J. 1986. Primary moult of adult Dunlins *Calidris alpina* of different age during autumn migration. Vår Fågelvärld. Suppl. 11: 51–56.
- Gromadzka J. 1989. Breeding and wintering areas of Dunlin migrating through southern Baltic. Ornis Scand. 20: 132–144.
- Hake M., Kjellen N. & Alerstam T. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. Oikos 103: 385–396.
- Harrington B.A., Leeuwenberg F.J., Resende S.L., McNeil R., Thomas B.T., Grear J.S. & Martinez E.F. 1991. Migration and mass change of White-Rumped Sandpipers in North and South-America. Wilson Bull. 103: 621–636.
- Hayman P., Marchant J. & Prater T. 1986. Shorebirds: An identification guide to the waders of the world. Houghton Mifflin Company, Boston.
- Helseth A., Lindström Å. & Stervander M. 2005. Southward migration and fuel deposition of Red Knots Calidris canutus. Ardea 93: 213–224.
- Holmes, R. T. 1966. Breeding ecology and annual cycle adaptations of Red-Backed Sandpiper (*Calidris alpina*) in Northern Alaska. Condor 68: 3–46.
- Jing K. 2005. Stopover ecology of shorebirds in Chongming Dongtan, Shanghai. PhD thesis, Fudan University, Shanghai, China.
- Jing K., Ma Z., Li B., Li J. & Chen J. 2007. Foraging strategies involved in habitat use of shorebirds at the intertidal area of Chongming Dongtan, China. Ecol. Res. 22: 559–570.
- Johnson C. 1985. Patterns of seasonal weight variation in waders on the Wash. Ring. Migrat. 6: 19–32.
- Lindström Å. 2003. Fuel deposition rates in migrating birds: causes, constraints and consequences. In: Berthold P., Gwinner E. & Sonnenschein E. (eds) Avian Migration. Springer-Verlag, Berlin, pp. 307–320.
- Lindström Å., Klaassen M., Piersma T., Holmgren N. & Wennerberg L. 2002. Fuel stores of juvenile waders on autumn migration in high arctic Canada. Ardea 90: 93–101.

- Ma Z.J., Li B., Zhao B., Jing K., Tang S.M. & Chen J.K. 2004. Are artificial wetlands good alternatives to natural wetlands for waterbirds? A case study on Chongming Island, China. Biodivers. Conserv. 13: 333–350.
- Ma Z.J., Tang S.M., Lu F. & Chen J.K. 2002. Chongming Island: A less important shorebird stopover site during southward migration? Stilt 41: 35–37.
- Mascher J.W. & Marcstrom V. 1976. Measures, weights, and lipid levels in migrating Dunlins *Calidris a. alpina* L. at the Ottenby Bird Observatory, South Sweden. Ornis Scand. 7: 49–59.
- Nettleship D.N. 2000. Ruddy Turnstone (*Arenaria interpres*). In: Poole A. and Gill F. (eds) The Birds of North America, no. 537. Academy of Natural Sciences, Philadelphia, and AOU, Washington, D.C.
- O'Reilly K.M. & Wingfield J.C. 1995. Spring and autumn migration in Arctic shorebirds: Same distance, different strategies. Am. Zool. 35: 222–233.
- Persson C. 2007. The Meissner ranking scale. http://www.bostream.nu/fagelstudier/textmapp/meissner.html, accessed on 26 Dec 2007.
- Pienkowski, M. W., C. S. Lloyd, and C. D. T. Minton. 1979. Seasonal and migrational weight changes in Dunlins. Bird Study 26: 134–148.
- Piersma T. 1987. Hop, skip or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. Limosa 60: 185–194.
- Piersma T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. J. Ornithol. 148 (Suppl.): S45–S59.
- Piersma T., van Gils J. & Wiersma P. 1996. Family Scolopacidae (sandpipers, snipes and phalaropes). In: Del Hoyo J., Elliott A. & Sargatal J. (eds) Handbook of the birds of the world. Lynx Edicions, Barcelona, pp. 444–533.
- Prater A.J., Marchant J.H. & Vuorinen J. 1977. Guide to the identification and ageing of Holarctic waders. BTO Field Guide 17, BTO, Tring, UK.
- Rimmer C.C. & McFarland K.P. 2000. Migrant stopover and post-fledging dispersal at a montane forest site in Vermont. Wilson Bull. 112: 124–136.
- Schaub M. & Jenni L. 2000a. Body mass of six long-distance migrant passerine species along the autumn migration route. J. Ornithol. 141: 441–460.
- Schaub M. & Jenni L. 2000b. Fuel deposition of three passerine bird species along the migration route. Oecologia 122: 306–317.
- Schaub M. & Jenni L. 2001a. Stopover durations of three warbler species along their autumn migration route. Oecologia 128: 217–227.
- Schaub M. & Jenni L. 2001b. Variation of fuelling rates among sites, days and individuals in migrating passerine birds. Funct. Ecol. 15: 584–594.
- Scheiffarth G., Wahls S., Ketzenberg C. & Exo K.M. 2002. Spring migration strategies of two populations of bar-tailed godwits, *Limosa lapponica*, in the Wadden Sea: time minimizers or energy minimizers? Oikos 96: 346–354.
- Schulte-Hostedde A.I., Zinner B., Millar J.S. & Hickling G.J. 2005. Restitution of mass-size residuals: Validating body condition indices. Ecology 86: 155–163.
- Shepherd P.C.F., Lank D.B., Smith B.D., Warnock N., Kaiser G.W. & Williams T.D. 2001. Sex ratios of Dunlin wintering at two latitudes on the Pacific coast. Condor 103: 352–360.

- SPSS Inc. 2003. SPSS for Windows version 12.0. SPSS Inc. Chicago.
- Swanson D.L., Liknes E.T. & Dean K.L. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant ruby-crowned kinglets. Wilson Bull. 111: 61–69.
- Tulp I., McChesney S. & de Goeij P. 1994. Migratory departures of waders from North-western Australia: Behaviour timing and possible migration routes. Ardea 82: 201–221.
- Warnock N.D. & Gill R.E. 1996. Dunlin (*Calidris alpina*). In: Poole A. & Gill F. (eds) The Bird of North America, no. 203. Academy of Natural Sciences, Philadelphia, and AOU, Washington, D.C.
- Wilson J.R. & Barter M.A. 1998. Identification of potentially important staging areas for 'long jump' migrant waders in the East Asian-Australasian Flyway during northward migration. Stilt 32: 16–28.
- Winker K. 1995. Autumn stopover on the Isthmus of Tehuantepec by woodland nearctic-neotropic migrants. Auk 112: 690–700.
- Winker K., Warner D.W. & Weisbrod A.R. 1992. Daily mass gains among woodland migrants at an inland stopover site. Auk 109: 853–862.
- Zar J.H. 1999. Biostatistical analysis, Prentice Hall, Upper Saddle River, New Jersey.
- Zwarts L., Ens B.J., Kersten M. & Piersma T. 1990. Moult, mass and flight range of waders ready to take off for long-distance migrations. Ardea 78: 339–364.

SAMENVATTING

In China pleisteren grote aantallen steltlopers die tussen het broedgebied in Noordoost-Azië en Alaska en het overwinteringsgebied in Oost-Azië en Australië trekken. Over de precieze betekenis van de Chinese pleisterplaatsen binnen de jaarcyclus van steltlopers is nog betrekkelijk weinig bekend. Het onderhavige onderzoek, uitgevoerd in Chongming Dongtan, een belangrijk wetland aan de oostkust van China, spitste zich toe op een vergelijking van lichaamsconditie en snelheid van aanleg van lichaamsreserves tussen een vijftal steltlopersoorten. Twee soorten, de Grote Kanoet Calidris tenuirostris en Kanoet C. canutus, zijn langeafstandstrekkers die tussen Chongming Dongtan en Australië een afstand overbruggen van ruim 5000 km. De andere drie soorten leggen minder grote afstanden af en overwinteren in de regio, te weten de Roodkeelstrandloper C. ruficollis, Taigastrandloper C. subminuta en de Bonte Strandloper C. alpina. De waargenomen verschillen tussen de soorten in lichaamsconditie en snelheid waarmee reserves werden aangelegd in Chongming Dongtan, kwamen overeen met de verwachting: langeafstandstrekkers leggen meer reserves aan dan vogels die slechts een korte afstand afleggen. Omdat de Bonte Strandloper in het voorjaar meer reserves aanlegt dan in het najaar, wordt verondersteld dat de voorjaarstrek begint met een forse sprong over de Gele Zee richting het broedgebied.

Corresponding editor: Julia Stahl Received 9 August 2008; accepted 2 February 2009

Online appendix is available at www.ardeajournal.nl

Appendix 1. Comparison of calidrid sandpipers' morphology between seasons (data from 2003–2007). Superscript letters show results from F-tests or Tukey HSD multiple comparison tests (P < 0.05). Different letters indicate significant differences between season/age-classes (P < 0.05). Given are means \pm SD, and sample sizes in parentheses. S: southward migration, N: northward migration.

Species	Season/age	Body mass (g)	Wing length (mm)	Bill length (mm)	Tarsus (mm)
Great Knot	First-year birds (S)	155 ± 22.8 ^a (241)	183 ± 4.9 ^a (241)	42.1 ± 2.0^{a} (240)	36.3 ± 1.3 ^a (241)
	Adults (N)	132 ± 13.7 ^b (5946)	190 ± 5.3 ^b (4926)	43.6 ± 1.9^{b} (4881)	37.7 ± 2.3 ^b (3369)
Red Knot	First-year birds (S)	105 ± 16.8 ^a (55)	161 ± 3.9 ^a (54)	31.7 ± 2.0^{a} (54)	31.7 ± 1.4^{a} (55)
	Adults (N)	98.8 ± 11.4 ^b (581)	168 ± 5.0 ^b (579)	32.7 ± 1.8^{b} (580)	32.6 ± 1.9^{b} (509)
Red-necked Stint	First-year birds (S)	25.3 ± 3.9 ^a (224)	102 ± 3.0^{a} (222)	17.5 ± 0.9 ^a (223)	$20.2 \pm 0.9 (224)$
	Adults (S)	28.6 ± 4.4 ^b (119)	103 ± 2.6^{b} (115)	17.8 ± 0.9 ^b (119)	$20.0 \pm 0.8 (118)$
	Adults (N)	26.5 ± 2.8 ^c (546)	104 ± 2.9^{c} (544)	17.7 ± 1.0 ^b (548)	$20.1 \pm 0.8 (512)$
Long-toed Stint	First-year birds (S) Adults (S) Adults (N)	24.1 ± 2.9^{a} (1312) 28.3 ± 4.6^{b} (280) 25.6 ± 2.9^{a} (22)	94.5 ± 2.4° (1314) 93.9 ± 2.6° (258) 95.2 ± 3.6° (23)	18.4 ± 0.9^{a} (1312) 18.5 ± 0.9^{b} (282) $18.4 \pm 1.1^{a,b}$ (23)	$22.7 \pm 1.0 (1312)$ $22.7 \pm 0.8 (282)$ $22.8 \pm 0.9 (23)$
Dunlin	First-year birds (S)	47.6 ± 4.9 ^a (457)	123 ± 3.2^{b} (460)	36.7 ± 2.7^{b} (452)	27.3 ± 1.1^{b} (458)
	Adults (S)	49.1 ± 5.7 ^a (73)	122 ± 3.2^{a} (73)	35.5 ± 2.6^{a} (74)	26.8 ± 0.9^{a} (73)
	Adults (N)	53.8 ± 6.4 ^b (983)	122 ± 3.8^{a} (924)	35.2 ± 2.6^{a} (932)	26.9 ± 1.3^{a} (776)

Appendix 2. Results of linear regressions for five calidrid species of bill and tarsus length with wing length during northward migration (southward migration for Dunlins).

Species		Bill length			Tarsus length			
	n	R	F	P	n	R	F	P
Great Knot	4854	0.244	308	< 0.001	3351	0.102	35.2	< 0.001
Red Knot	579	0.352	81.6	< 0.001	508	0.245	32.4	< 0.001
Red-necked Stint	542	0.305	55. 6	< 0.001	506	0.228	27.5	< 0.001
Long-toed Stint	23	0.584	10.9	0.003	23	0.297	2.03	0.169
Dunlin	73	0.403	13.8	< 0.001	72	0.345	9.45	0.003



TIJDSCHRIFT DER NEDERLANDSE ORNITHOLOGISCHE UNIE (NOU)

ARDEA is the scientific journal of the Netherlands Ornithologists' Union (NOU), published bi-annually in spring and autumn. Next to the regular issues, special issues are produced frequently. The NOU was founded in 1901 as a non-profit ornithological society, composed of persons interested in field ornithology, ecology and biology of birds. All members of the NOU receive ARDEA and LIMOSA and are invited to attend scientific meetings held two or three times per year.

NETHERLANDS ORNITHOLOGISTS' UNION (NOU)

Chairman – J.M. Tinbergen, Animal Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands **Secretary** – P.J. van den Hout, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands (hout@nioz.nl)

Treasurer - E.C. Smith, Ir. van Stuivenbergweg 4, 6644 AB Ewijk, The Netherlands (ekko.diny@planet.nl)

Further board members - E. Boerma, G.J. Gerritsen, J. Komdeur, J. Ouwehand, G.L. Ouweneel, J.J. de Vries

Membership NOU – The 2009 membership fee for persons with a postal address in The Netherlands is €42 (or €25 for persons <25 years old at the end of the year). Family members (€9 per year) do not receive journals. Foreign membership amounts to €54 (Europe), or €65 (rest of the world). Payments to Postbank account 285522 in the name of Nederlandse Ornithologische Unie, 8897HZ Oosterend-Terschelling, The Netherlands (BIC: PSTBNL21 and IBAN: NL85 PSTB 0000 285522). Payment by creditcard is possible. Correspondence concerning membership, payment alternatives and change of address should be sent to: J.J. de Vries, Oosterend 10 b, 8897 HZ Oosterend-Terschelling, The Netherlands (jacobird@xs4all.nl).

Research grants – The NOU supports ornithological research and scientific publications through its Huib Kluijver Fund and the 'Stichting Vogeltrekstation'. Applications for grants can be addressed to the NOU Secretary. Donations to either fund are welcomed by the NOU treasurer.

Internet - www.nou.nu

ARDEA

Editors of ARDEA – Rob G. Bijlsma, Wapse (Editor in chief); Christiaan Both, Groningen; Niels J. Dingemanse, Groningen; Dik Heg, Bern; Ken Kraaijeveld, Leiden; Jouke Prop, Ezinge (Technical editor); Julia Stahl, Oldenburg; B. Irene Tieleman, Groningen; Yvonne I. Verkuil, Groningen

Dissertation reviews - Popko Wiersma, Groningen

Editorial address – Jouke Prop, Allersmaweg 56, 9891 TD Ezinge, The Netherlands (ardea.nou@planet.nl)

Graphics - Dick Visser, Haren

Artwork - Jos Zwarts, Bunnik

Internet - www.ARDEAjournal.nl

Subscription *ARDEA* – Separate subscription to Ardea is possible. The 2009 subscription rates are €35 (The Netherlands), €41 (Europe), and €49 (rest of the world). Institutional subscription rates are €52, €67, and €76, respectively). Payments to Postbank account 125347, in the name of Nederlandse Ornithologische Unie, Ir. van Stuivenbergweg 4, 6644 AB Ewijk, The Netherlands (BIC: PSTBNL21 and IBAN: NL65 PSTB 0000 125347). Correspondence concerning subscription, change of address, and orders for back volumes to: J.J. de Vries, Oosterend 10 b, 8897 HZ Oosterend-Terschelling, The Netherlands (jacobird@xs4all.nl).

Exchange of publications – All periodicals sent in exchange for *ARDEA* should be addressed to: Library of the Netherlands Ornithologists' Union (NOU), c/o Tineke Prins, Institute of Systematics and Population Biology, Zoological Museum, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands.

Books for review – should be addressed to: *ARDEA* Secretariat, c/o J. Prop, Animal Ecology Group, Biological Centre, P.O. Box 14, 9750 AA Haren, The Netherlands. After review, the books will be deposited in the NOU Library in Haren.

NOU Library (journals) - Mauritskade 57, Amsterdam, Mo-Fr 10:00-16:00 (to check in advance by telephone + 31 20 525 6614).

NOU Library (books) – Library Biological Centre, Kerklaan 30, Haren (G.), Mo–Thu 09:00–17:00 (to check at www.rug.nl/bibliotheek/locaties/bibfwn/index).

© Nederlandse Ornithologische Unie (NOU), 2009 Layout by Dick Visser, Haren, The Netherlands Printed by Van Denderen, Groningen, The Netherlands, April 2009 Downloaded From: https://complete.bioone.org/journals/Ardea on 21 Sep 2024 Terms of Use: https://complete.bioone.org/terms-of-use