

Body condition of shorebirds upon arrival at their Siberian breeding grounds

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Abstract Arctic breeding shorebirds carry substantial body stores on their long-distance migrations from their non-breeding grounds. Upon arrival at the breeding area the remains of these stores can be used for egg formation, insurance against poor feeding conditions or rebuilding organs. We quantified body condition (body mass, total body water, lean body mass and fat mass estimated using the deuterium dilution method) in seven shorebird species caught upon arrival in the Siberian Arctic. Arrival condition was compared with incubation condition in a subset of

species. After correction for structural size, body mass was significantly lower at arrival than during incubation in most of the species (but 3–18% above lean mass). Fat index (fat mass/lean mass) varied between 5.1 and 13.2%. Fat stores were estimated to enable survival for 0.6 days for the smallest and 2.5 days for the largest species. We discuss possible functions of arrival stores: insurance, egg-formation or rebuilding organs.

Keywords Arctic · Taimyr · Shorebirds · Body mass · Fat · Lean mass

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Introduction

Arctic breeding birds generally undertake long migrations from their non-breeding areas to the breeding grounds. The Arctic summer is short and the time available for finding a mate, laying eggs, raising chicks and preparing for return migration comprises hardly more than 2 months. Within this short period, food availability usually shows a short seasonal peak, particularly for birds that feed on invertebrates living on the tundra surface (MacLean and Pitelka 1971; Tulp and Schekkerman 2008). An optimal use of the short breeding season is therefore essential for successful reproduction.

For many arctic-breeding birds, an early arrival on the tundra in a condition that allows a quick start of breeding may maximise reproductive success. The fact that a correlation between arrival stores and the timing of breeding among individual shorebirds has not been shown until now might well be caused by the logistic difficulties of such measurements in the field. An early arrival however, may also incorporate a risk for arctic birds: the tundra may still be snow-covered and frozen and offer no food to arriving birds.

One way to overcome this risk is to bring enough body stores to the tundra to both survive without having to feed and produce eggs. This strategy ('capital breeding') is used by some of the larger arctic-breeding geese (Meijer and Drent 1999). They store enough nutrients at their last spring staging site not only to complete the migratory journey, but also to produce eggs and sustain part of the females' metabolism during incubation. On theoretical grounds, shorebirds, of which many species undertake similarly long or even longer migrations than geese, are less likely to use this strategy, because of their much smaller size (Klaassen 2003). Empirical studies comparing isotope signatures of eggs with body stores accumulated during migration (Morrison and Hobson 2004) and chicks with those of feathers grown by their parents on wintering or spring staging areas (Klaassen et al. 2001), have confirmed that arctic shorebirds generally produce eggs mostly from nutrients collected after arrival on the breeding grounds ('income breeders'; (Klaassen et al. 2001; Morrison and Hobson 2004; Morrison et al. 2005).

Instead of being channelled into eggs, nutrient stores carried to the breeding grounds may also be metabolised during the period directly after arrival, when food availability is limited and unpredictable owing to weather and snow conditions (Morrison 1975; Sandberg 1996; Baker et al. 2004; Morrison et al. 2005). Such stores may be important for survival and reproduction: unusually cold early summers in 1972 and 1974 caused extensive mortality of adult Red Knots *Calidris canutus* in northern Greenland and Canada (Morrison 1975; Boyd and Piersma 2001), and birds departing from Iceland with below-average mass suffered more than heavier birds (Morrison 2006; Morrison et al. 2007). In 1999, when snow melt was late at Alert, Canada, arrival masses were significantly lower than the long-term mean and many shorebirds postponed breeding or did not breed at all (Morrison et al. 2005).

Arrival stores may also be used to rebuild organs that were reduced for the migratory flight but are needed during reproduction. Red Knots and Ruddy Turnstones *Arenaria interpres* arrived at Ellesmere Island (Canada) with relatively large fat and muscle stores (Morrison and Davidson 1990; Morrison et al. 2005). During the post-arrival period these stores declined in size while the digestive system, heart and liver increased, indicating that a key function of the stores was to enable a physiological transformation into suitable breeding condition at a time of the year when food was scarce (Morrison et al. 2005).

Hence, even if eggs are formed from locally acquired nutrients, the energy stores that arctic shorebirds carry upon arrival on their breeding grounds can still be functional for reproduction (Sandberg and Moore 1996). In preparation for migratory flight, long-distance migrant shorebirds change their body composition: digestive organs

not needed during the flight are reduced in size to reduce the weight, while flight muscles gain in mass and fat stores are built up. Upon arrival the digestive organs regain their original size (Piersma and Gill 1998; Piersma et al. 1999; Battley et al. 2000; Morrison et al. 2005). These transformations involve rapid changes in protein and fat contents. In view of these dynamics of organ size during pre-migratory fattening, migration, and post-arrival, it is useful not only to have insight into the total arrival mass, but also in the relative proportion of fat stores and lean tissue.

Owing to the difficulties of capturing birds directly upon arrival, little empirical data are available on dynamics of body mass and nutrient stores in this period. Published studies have been carried out in Nearctic areas only (Morrison and Davidson 1990; Farmer and Wiens 1999; Morrison et al. 2005; Krapu et al. 2006). In this study we describe variation in the arrival condition of several Palearctic shorebird species on the arctic tundra of the Taimyr Peninsula, Siberia, Russia. The total body mass was measured in all species. In a selection of species lean (fat-free) mass and fat mass were estimated with the deuterium dilution method (Speakman et al. 2001). We compare body condition (total body mass, lean mass, fat stores) on arrival with that at other times of the year, and explore the potential value of the energy stores. Because pre-migratory accumulation and migratory depletion of nutrient stores are known to involve not only fat but also proteins in muscles and other body organs (Piersma and Gill 1998; Piersma et al. 1999; Battley et al. 2000), lean mass does not provide a constant yardstick for comparing stores between individuals or between different phases of the annual cycle. Therefore we compared our observations with the mean mass of the studied species in their African non-breeding quarters, representing a part of the annual cycle when no pre-migratory fattening takes place and birds carry only small energy stores as insurance against periods of hardship. In species that allow comparison between the sexes, we checked for differences between sexes in arrival stores, since such differences are expected if arrival stores play a role in egg formation (Sandberg and Moore 1996, Smith and Moore 2003).

Study site

Data were collected between June and mid-August of 2000, 2001 and 2002 at Medusa Bay, 18 km south of Dikson on the west coast of the Taimyr Peninsula, Siberia, Russia (73°20' N 80°30' E). The habitat can be characterised as arctic tundra (cf Chernov 1985). Vegetation consists of moss, lichen, grass, sedge, and dwarf willow generally <20 cm, with a significant proportion of the surface bare ground. The landscape has a rolling relief with scattered stony ridges. For a more detailed description see

Schekkerman et al. (2004). Snow melt in the study area usually started 5–12 June, and most egg-laying of shorebirds occurred between 15 June and 10 July. Shorebird species that pass through but also breed at the site include Eurasian Dotterel *Charadrius morinellus*, Little Stint *Calidris minuta*, Dunlin *C. alpina*, Curlew Sandpiper *C. ferruginea*, Pectoral Sandpiper *C. melanotos*, Red Phalarope *Phalaropus fulicarius* and Ruddy Turnstone. Species that pass through but only breed up to several hundreds of kilometres farther north and east on the peninsula include Red Knot, Sanderling *C. alba* and Purple Sandpiper *C. maritima*.

Methods

Catching arriving birds

During the first 2 weeks of the arctic spring (6–16 June 2000, 6–20 June 2001, 9–22 June 2002) we caught shorebirds that had just arrived on the breeding grounds, using a clap net. The net measured 10 × 1.5 m and was released by an elastic mechanism upon pulling a line from a distance of 20–30 m. Birds were lured to the net by decoys and playback of shorebird vocalisations. The net was set-up in snow-free patches adjoining the snow edge. Snow edges provide foraging habitat for newly arriving shorebirds. Birds were caught either when they landed within reach of the net or walked within reach after landing nearby, or while they were flying slowly over the net at low altitude. No predefined selection of target species was made and we attempted to catch every shorebird that was attracted to the net.

In the arrival period, Red Phalaropes foraging in small pools were caught by using mist nets held horizontally between two observers while approaching the birds downwind. Phalaropes swam away until they reached the end of the pool and then either stopped apparently undecided about what to do until the net was laid on top of them, or they flew up into the wind and could be caught by flipping the net upwards.

Catching birds during incubation

Incubating birds were caught on their nest. Nests were located by intensive searching during and after the laying period and marked using GPS. Birds were caught using small clap nets (diameter ca 40 cm) set up over the nest and released by the bird itself when it returned to sit on the eggs. To avoid nest desertion we only caught birds on the nest from the second week of incubation onwards. The stage of incubation was estimated by egg flotation (Liebezeit et al. 2007).

Biometric measurements

Captured birds were ringed with metal rings and measured. Bill length was measured to the nearest 0.1 mm using callipers. Wing length (maximum chord, 1 mm) was measured with a stopped ruler. Spring balances were used to measure total body mass (to 0.1 g). Most birds were weighed within 10 min of capture, and all within 30 min. Dunlins, Curlew Sandpipers, Ruddy Turnstones and Red Phalaropes were sexed on plumage characteristics and size. Red Knots, Little Stints and Eurasian Dotterels could not be reliably sexed on external characters.

Deuterium measurements

Measurements of total body water (TBW) were used to separate total body mass into fat mass and lean mass. TBW was measured using the deuterium dilution method (Lifson and McClintock 1966; Speakman 1997; Visser et al. 2000; Speakman et al. 2001) in a subset of the Curlew Sandpipers, Eurasian Dotterels, Dunlins, Red Knots, Little Stints, Sanderlings and Ruddy Turnstones caught upon arrival (see Tables 1, 2 for sample sizes). In addition to data collected during this study, TBW measurements of incubating Little Stints and Dunlins collected in 2000–2002 and published elsewhere (Tulp and Schekkerman 2008) were also used.

Captured birds were injected subcutaneously near the pectoral muscle with 0.10–0.30 ml of water (i.e. a dose of 3.3 mg/g bird, SD = 0.591) consisting of 42.1% D₂O (dose Q_d , converted to moles administered). Subsequently biometrical measurements and body mass were recorded and the birds were kept in a bag for 1 h. After this equilibration period four to six 10–15 µl blood samples were collected from a vein in the wing, in glass capillary tubes which were flame-sealed within minutes. In three adults of each species and year a set of blood samples was taken before injection, to assess species-specific background concentrations (C_{back} , atom percent) of ²H. Samples were analysed in triplicate at the Centre for Isotope Research at Groningen University in The Netherlands, using vacuum distillation of the blood samples, conversion of the body water to H₂ gas, and assessment of ²H/¹H isotope ratios with a SIRA9 isotope ratio mass spectrometer. We used internal ²H₂O laboratory standards with different enrichments, as well as a dilution sample of the dose. For further details see Visser et al. (2000). TBW (g) was calculated based on the quantitative injection of the isotope mixture (Q_d , moles), the year- and species-specific ²H background concentration (C_{back} , atom percent), and the individual-specific ²H enrichment of the equilibration sample (C_{eq} , atom

Table 1 Mean body mass (g) of shorebirds caught at Medusa Bay, Taimyr Peninsula, Russia, in 2000–2003 (with standard deviation, range and sample size)

Species	Arrival						Incubation				
	Sex	Mean	SD	Min	Max	<i>n</i>	Mean	SD	Min	Max	<i>n</i>
Eurasian Dotterel	All	124.5	7.2	112.0	140.0	26	110.5	0.7	110.0	111.0	2
Red Knot	All	130.1	8.1	120.0	138.5	5					
Sanderling	Male	48.5	4.9	45.0	52.0	2					
Little Stint	All	26.0	3.6	20.5	36.2	22	29.1	2.6	23.7	37.3	235
Curlew Sandpiper	All	58.4	4.0	51.0	68.5	36					
	Female	60.4	4.5	53.0	68.5	16	64.7	4.2	56.5	72.3	28
	Male	56.8	2.7	51.0	60.5	20					
Dunlin	All	48.9	3.9	41.8	57.1	28	53.3	3.5	45.5	62.0	81
	Female	51.9	3.4	45.3	57.1	9	54.9	3.3	48.2	62.0	37
	Male	47.4	3.3	41.8	54.5	19	51.9	3.2	45.5	60.5	42
Purple Sandpiper	All	69.3	0.1	69.2	69.3	2					
Red Phalarope	All	58.3	8.0	46.3	71.0	16					
	Female	61.1	6.9	50.5	71.0	12					
	Male	49.8	4.1	46.3	54.7	4	50.9	6.2	40.0	59.0	7
Ruddy Turnstone	All	102.5	8.3	94.0	123.0	15	101.4	5.7	97.7	108.0	3
	Female	108.9	9.9	95.0	123.0	6	108.0		108.0	108.0	1
	Male	98.3	2.9	94.0	103.0	9	98.1	0.6	97.7	98.5	2

Means are given for age and sex classes separately, and for the arrival and incubation phase. Recaptured birds are included only once (first capture) within each phase

percent) according to the formula for the ‘plateau-method’ (Speakman 1997):

$$TBW = 18.02 \cdot Q_d \cdot (42.1 - C_{eq}) / (C_{eq} - C_{back}).$$

These values were corrected for the slight but systematic overestimation of the deuterium dilution method relative to other methods for the assessment of the amount of body water (Speakman et al. 2001). Assuming that lean mass contains 69% water (Piersma and van Brederode 1990; Speakman et al. 2001; Eichhorn and Visser 2008, see Discussion for a sensitivity analysis of this assumption), lean (fat-free) body mass was calculated as:

$$\text{lean mass (g)} = TBW(\text{g})/0.69$$

and mass of the fat store subsequently as total body mass minus lean mass.

Statistical analyses

For each species, we calculated mean total body mass of all birds caught upon arrival, and compared that with the masses measured in the study area during the incubation phase and with published mean values from the species’ non-breeding areas (Red Knot 119 g, Sanderling 47 g, Little Stint 22 g, Curlew Sandpiper 52 g (Zwarts et al. 1990); Ruddy Turnstone 99 g (Ens et al. 1990); Dunlin: 47 g (Van der Have 1997); Eurasian Dotterel: 110 g

(Cramp and Simmons 1983). The total body mass upon arrival was compared with the total body mass during incubation after correcting for possible effects of structural size, using multiple linear regression. The best fitting structural measurement (wing, bill or total head length) was used to correct for structural size, after which effects of phase (arrival vs. incubation) or sex was tested. Due to a small sample size of some species in the incubation phase, comparisons were only carried out for Little Stint, Dunlin and Curlew Sandpiper (best fitting structural measurement for Little Stint: wing length, Dunlin: bill length, Curlew Sandpiper: total head length). Despite the small sample sizes, we include descriptive data on the other species (Eurasian Dotterel, Ruddy Turnstone) in this paper, given the scarcity of such information in the literature.

Second, we estimated lean mass and fat stores for the subset of birds in which TBW measurements were made, and compared these between phases of reproduction and between sexes. In Dunlin, Little Stint and Curlew Sandpiper sufficient TBW measurements were made to carry out regressions (cut-off arbitrarily chosen at >4 data points per phase/sex), again after correcting for the effect of structural size. The effect of phase (arrival vs. incubation) was included in the regressions for Dunlin and Little Stint; no TBW measurements were made during the incubation phase in Curlew Sandpiper.

Table 2 TBW measurements and derived lean mass and fat mass of shorebirds at Medusa Bay, Taimyr Peninsula, Russia. Sample size, mean total body mass, TBW, lean mass, fat mass (plus standard deviation and range) and fat index (fat mass/lean mass) are given per species and phase

Phase	n birds	Total body mass (g)					TBW (%)					Lean mass					Fat mass (g)					Fat index	
		Mean	SD	Min	Max		Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	
Dotterel	8	121.4	7.4	112.0	130.0	65.4	1.5	63.4	67.2	113.4	7.9	103.8	122.5	6.3	2.6	3.2	10.6	5.6					
Red Knot	3	126.0	7.9	120.0	135.0	61.2	4.4	56.7	65.4	109.9	4.7	105.5	114.9	14.5	8.9	6.4	24.1	13.2					
Sanderling	2	48.5	4.9	45.0	51.9	64.0	0.3	63.8	64.2	44.3	4.2	41.3	47.3	3.5	0.6	3.1	3.9	8.0					
Little Stint	16	25.3	2.5	21.9	31.3	65.8	4.0	56.1	70.1	23.7	2.4	20.3	30.6	1.2	1.6	-0.4	4.9	5.1					
	11	28.7	1.8	25.7	32.0	66.2	4.7	57.5	72.2	27.0	1.7	24.0	29.9	1.2	2.1	-1.3	5.2	4.5					
Curlew sandpiper	24	59.0	4.5	51.0	68.5	63.7	2.7	57.9	70.3	53.6	3.6	48.0	61.1	4.6	2.5	-1.1	10.7	8.6					
Dunlin	4	48.4	3.4	45.0	53.0	63.8	3.8	61.5	69.4	44.0	2.1	42.2	46.6	3.8	2.7	-0.3	5.7	8.6					
	9	52.2	4.7	44.3	59.2	66.8	3.7	59.9	71.1	49.7	3.4	44.9	55.4	1.8	3.0	-1.3	7.2	3.7					
Turnstone	8	102.9	9.4	95.0	123.0	62.2	3.3	57.5	67.3	91.2	7.0	83.4	105.9	10.3	5.4	2.3	18.2	11.3					

Results

Arrival mass

In seven species for which published total body mass values are available from their African non-breeding grounds, mean arrival mass in Taimyr was on average 9.0% (SD 5.9%, $N = 7$) above mean African non-breeding mass. This difference was smallest in Ruddy Turnstone (3.1%) and largest in Little Stint (17.6%) (Fig. 1a, b, Table 1). In most species arrival body mass varied among individuals between values as low as non-breeding mass to as high as incubation mass. Little Stint and Red Phalarope showed the largest variation in body mass among individuals (CV = 10.0 and 13.8% respectively), while Dotterel, Dunlin, Curlew Sandpiper and Ruddy Turnstone showed less variation (CV = 5.8, 6.6, 6.5 and 5.7% respectively).

Body mass in arriving versus incubating birds

After correction for wing length, arriving Little Stints weighed significantly less than incubating individuals (wing length $F_{1,227} = 25.14$, $P < 0.001$, phase: $F_{1,227} = 34.59$, $P < 0.001$, Fig. 1a). In Dunlin females were significantly heavier than males and both sexes weighed less upon arrival than during incubation (bill: $F_{1,103} = 33.03$, $P < 0.001$, sex: $F_{1,103} = 5.73$, $P_p = 0.019$, phase: $F_{1,103} = 34.19$, $P < 0.001$, Fig. 1a). Restricting the analysis to arriving birds only, the difference between the sexes was not significant after correction for bill length (bill: $F_{1,26} = 13.25$, $P = 0.001$, sex: $F_{1,26} = 0.55$, $P = 0.467$).

Because Curlew Sandpiper males do not incubate and were therefore only caught in the arrival period, we restricted the comparison between phases to females. Incubating females were significantly heavier than females that had just arrived (total head: $F_{1,42} = 1.16$, $P = 0.287$; phase: $F_{1,42} = 182.83$, $P = 0.003$, Fig. 1a). Among arriving birds, females were significantly heavier than males ($F_{1,32} = 8.99$, $P = 0.005$) while total head did not improve the model ($F_{1,32} = 2.94$, $P = 0.096$). Total head and sex were equally good explanatory variables for body mass.

The Eurasian Dotterels caught in the arrival period were all heavier than the two incubating males caught later in the season (not tested, Fig. 1b). In Red Phalarope, although females weighed more than males on arrival, there was no difference in arrival mass between sexes after correction for structural size (wing: $F_{1,13} = 8.79$, $P = 0.011$, sex: $F_{1,13} = 0.57$, $P = 0.462$). In males (the incubating sex), mass at arrival did not differ from that of incubating birds (wing: $F_{1,8} = 3.67$, $P = 0.092$, phase: $F_{1,8} = 0.18$,

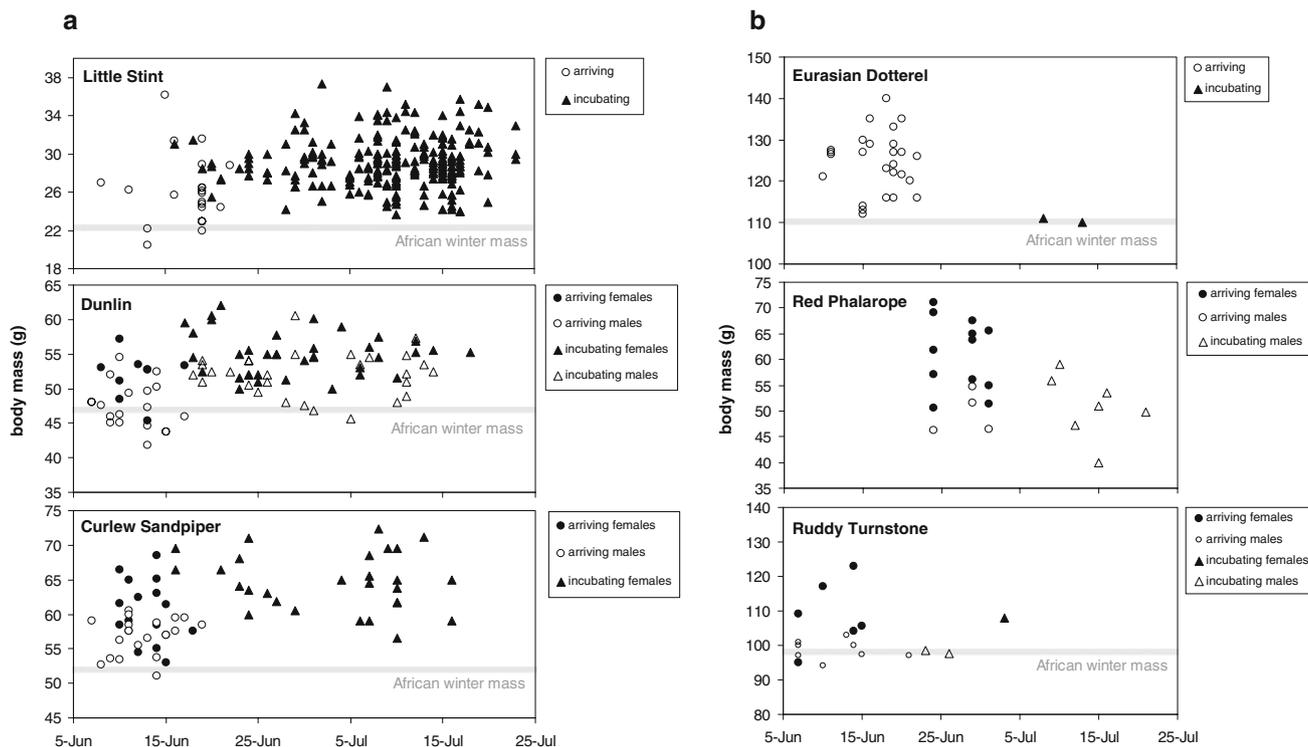


Fig. 1 **a** Body mass of Little Stint, Dunlin and Curlew Sandpiper caught during arrival and incubation and on non-breeding grounds in Africa (Zwarts et al. 1990; Van der Have 1997). **b** Body mass of Eurasian Dotterel, Red Phalarope and Ruddy Turnstone in relation to

catching date for birds caught during arrival, incubation and on non-breeding grounds in Africa (Cramp and Simmons 1983; Ens et al. 1990). For Red Phalarope no non-breeding mass values are available

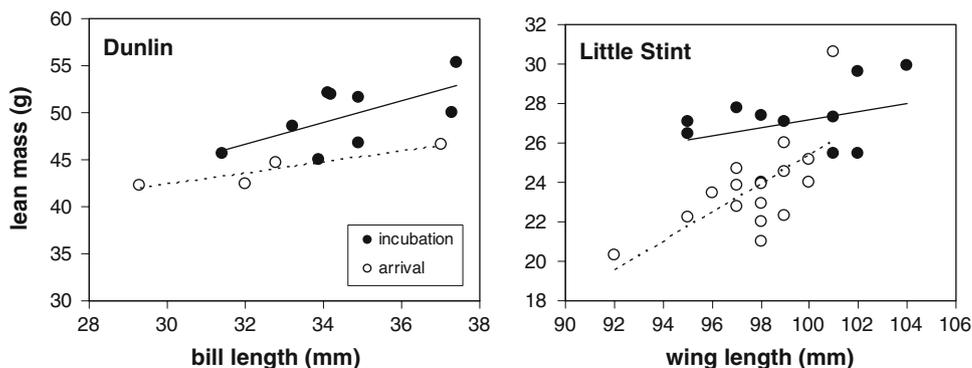
$P = 0.682$, Fig. 1b). Within the arrival period female Ruddy Turnstones weighed significantly more than males (wing $F_{1,13} = 0.59$, $P = 0.456$, sex $F_{1,13} = 9.43$, $P = 0.009$). Insufficient weights were taken in the incubation period for a formal comparison, but arriving birds tended to be heavier than incubating ones (Fig. 1b).

Lean mass and fat store

The average lean mass at arrival in Taimyr as determined by the isotope dilution method in seven species (Table 2) was on average 1.9% (SD 6.5%, $N = 7$) below the mean winter

mass of the same species in Africa. Compared to this yardstick, lean mass upon arrival was lowest in Ruddy Turnstone (-7.9%) and highest in Little Stint ($+7.9\%$). In Dunlin and Little Stint lean mass was measured in both arriving and incubating birds (Table 2). After correction for structural size, lean mass was significantly greater during incubation than upon arrival in both species (Table 2, Fig. 2). After correction for size, there was no difference between the lean mass of arriving female and male Curlew Sandpipers (total head length: $F_{1,22} = 14.68$, $P = 0.001$, sex $F_{1,22} = 0.52$, $P = 0.480$). In Dunlin the sample size of arriving birds was too small to test for a sex effect.

Fig. 2 Lean mass in relation to indices of structural size for Dunlin and Little Stint in the arrival versus the incubation phase



To compare fat stores across species and phases we expressed fat stores as an index (fat mass/lean mass) (Table 2). For the seven species, the fat index upon arrival was on average 7.6% (SD = 3.2%, $N = 7$, Table 2). It varied among species from 5.1% in Little Stint to 13.2% in Red Knot, and was not significantly related to the species' lean mass ($F_{1,5} = 1.75$, $P = 0.24$). Fat stores did not differ significantly between arriving and incubating Little Stints (wing: $F_{1,25} = 0.16$, $P = 0.691$, phase: $F_{1,25} = 0.01$, $P = 0.938$, Fig. 3). Fat stores of Dunlin did not differ between the arrival and incubation phases nor between the sexes (bill: $F_{1,11} = 0.05$, $P = 0.832$, sex: $F_{1,11} = 1.37$, $P = 0.266$, phase: $F_{1,25} = 1.16$, $P = 0.305$). Arrival fat stores in Curlew Sandpiper did not differ significantly between the sexes (total head: $F_{1,22} = 0.07$, $P = 0.795$, sex: $F_{1,22} = 0.00$, $P = 0.994$).

Discussion

Our observations add significantly to the existing volume of data on body condition of shorebirds arriving on their arctic breeding grounds. Migratory body and organ mass dynamics have been well-studied in several shorebird species, but the remoteness of their breeding grounds and the difficulty of catching adequate samples of birds before they spread out across the vast tundra have led to little data being collected from this important stage of the annual cycle.

Our capture method of using clap net and tape lures was successful in trapping recently arrived shorebirds and birds

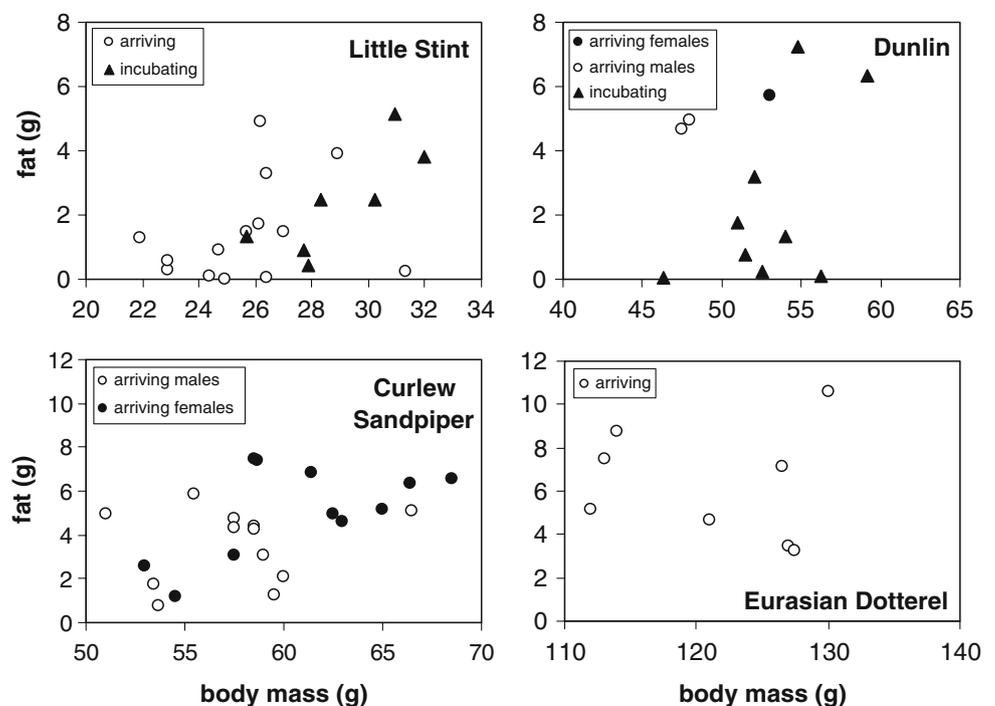
completing the last part of their migratory flight. The appearance of certain species such as Curlew Sandpiper and Little Stint, within the study area was quite sudden, and most of our catches closely followed this moment of arrival. Once birds started to display territorial and courtship behaviour, they were less easily attracted to the nets. An exception to this was the Eurasian Dotterel of which individuals often overflow the study area apparently looking for mates and were strongly attracted to the played-back sound of displaying conspecifics.

The purpose of this study was to catch shorebirds arriving after their long-distance flight on their breeding grounds. But how sure can we be that we really caught birds right on arrival? Several observations from the field indicate that arrival is not as clear-cut as we thought at the beginning of the study.

What is 'arrival'?

A proportion of the trapped birds was observed that descended from high altitudes in response to the play-backs or which were trapped in flight when they were flying low above the ground into northeasterly winds. Our sample therefore probably consisted not only of birds that had the intention to stop at our study site, regardless of the attraction of the play-backs, but also of birds that would have moved on had they not been attracted by the sounds. Therefore we cannot be certain that all of the birds caught had reached their final destination. Species like Curlew Sandpiper, Little Stint, Dunlin, and Ruddy Turnstone all

Fig. 3 Fat mass as estimated from TBW measurements in relation to total body mass for Little Stint, Dunlin, Curlew Sandpiper and Eurasian Dotterel



breed in the study area but have a wide breeding distribution and may have moved on after capture. Of species that do not or only rarely breed in the area, like Sanderling, Red Knot and Eurasian Dotterel, we are almost certain that they had not reached their breeding area yet. However, all these birds must have been on the final leg of their migration, with their breeding destination at most 1,000 km away (northeastern tip of the Taimyr Peninsula). This would mean that the average distance yet to be covered was perhaps 10% of the total (great circle) distance between ultimate spring stopover sites in NW-Europe and SW-Siberia (ca 4,800 km; Henningsson and Alerstam 2005). For this group of birds, the possibility exists that the trapping method resulted in a non-random selection of birds. Individuals with depleted reserves might be more prone to interrupt their flight in response to the tape lures than birds that still have enough reserves left to continue their journey northward. While we cannot exclude this possibility, we note that individuals that descended from higher altitudes included both birds that had depleted their reserves completely as well as birds with reserves left.

We also suspect that some shorebirds arriving at Medusa Bay as their final destination may have previously stopped for a few days in snow-free tundra patches further south. Two observations suggest that this may have happened. The arctic spring of 2002 was delayed with snow cover dropping below 50% 9 days later than in 2000–2001. In the first half of June 2002 we counted numbers of staging shorebirds in our study area that exceeded the number later found breeding for several species. These birds disappeared as soon as warmer weather initiated snow melt (Schekkerman et al. 2004). Ring-reading showed that in Dunlin this early wave consisted of non-local birds, as 50% of the site-faithful local birds had been individually colour-marked in the previous years. Colour-marked Dunlin arrived on average 6 days later in 2002 than in 2001 and started laying 7 days later (Schekkerman et al. 2004). These observations suggest that shorebirds arriving in Taimyr may not always fly directly to their previous year's breeding site but adjust their progress to local snow conditions by making one or more stops short of their final destination. This is also substantiated by Frodin et al. (1994) who suggest that Curlew Sandpipers already paired at waiting sites south of their final breeding sites. In continental tundra areas like Taimyr, 'arrival' should perhaps not be considered a discrete process in the way that it may be in areas where shorebirds arrive after a long-distance flight across a large ecological barrier with few or no options for stopping en route, like Greenland. In conclusion, our sample probably consisted of a mixture of birds including individuals that had reached their final destination, and 'arrival on the breeding grounds' can probably not be regarded as a discrete point along an individual's migration route.

General patterns in arrival condition

The average fat index (fat mass/lean mass) of waders arriving in Taimyr varied between species from 5 to 13%. The body mass of shorebirds wintering in West Africa comprises about 3–8% fat on average (Zwarts et al. 1990). The average body mass of waders arriving in Taimyr was 3–18% (mean 9%) above the African winter mass of these same species. The average lean mass on arrival was between 8% below and 8% above the mean African winter mass (mean 2% below), and thus on average slightly (ca 5%) above the lean mass of the African non-breeding birds. On average therefore, shorebirds arrived in Taimyr with some energy stores remaining, but generally not a large amount. However, these averages mask a large variation between individuals (Fig. 1a, b). This variation may arise from differences in body condition at departure from the last staging area, in conditions encountered and/or metabolic efficiency during the migratory flight, or in the period that birds had been already present in the Arctic and the conditions encountered there.

In our calculation of fat and lean mass we assumed that the lean mass consists of 69% water, based on an average of values reported in literature (Piersma and van Brederode 1990; Eichhorn and Visser 2008). Because water content of fat-free tissues can vary both between and within individuals, we carried out a sensitivity analysis, using the range of variation in water content reported in literature for shorebirds and waterfowl (Piersma and van Brederode 1990; Eichhorn and Visser 2008; Newton 2008). Piersma and van Brederode (1990) illustrated that a large part of the observed variation is caused by the time between capture and weighing, because trapped birds lose water faster than they metabolise nutrient stores. In our study weighing was always carried out within 30 min after capture; therefore, we limited the sensitivity analysis to a range of 67–73%, values reported during the first 2 h after capture by Piersma and van Brederode (1990). The resulting mean fat content shows considerable sensitivity to the water content of lean tissue, i.e. between 0.5 and 2.5 g for Little Stint, between 2.4 and 6.2 g for Dunlin and between 3.0 and 7.6 g for Curlew Sandpiper (Table 3). These values are however still in the same order of magnitude as the fat contents calculated using a water content of 69%, and therefore our main findings do not strongly depend on this assumption. Because the lean mass made up a considerably larger fraction of the total body mass than the fat mass in our shorebirds, the relative effects of using different values of water content on the lean mass are smaller than for those on the fat mass (Table 3).

Studies in the Nearctic have also described fat stores upon arrival. Morrison et al. (2005, and see Morrison 2006), who caught and collected Red Knots upon arrival

Table 3 Sensitivity of estimates of lean mass and fat mass to assumptions for water content of lean mass. A range between 67 and 73% was applied (Piersma and van Brederode (1990) and compared to the value of 69% that was used in our calculations

		Fat and lean mass based on water content of lean mass					
		69%		67%		73%	
		Fat mass	Lean mass	Fat mass	Lean mass	Fat mass	Lean mass
Eurasian Dotterel	Spring migration	6.3	113.4	2.9	128.1	12.6	110.3
Red Knot	Spring migration	14.5	109.9	11.2	124.1	20.6	106.9
Sanderling	Spring migration	3.5	44.3	2.2	50.0	6.0	43.1
Little Stint	Spring migration	1.2	23.7	0.5	26.8	2.5	23.1
	Incubation	1.2	27.0	0.4	30.5	2.7	26.3
Curlew Sandpiper	Spring migration	4.6	53.6	3.0	60.6	7.6	52.1
Dunlin	Spring migration	3.8	44.0	2.4	49.6	6.2	42.8
	Incubation	1.8	49.7	0.3	56.1	4.6	48.3
Ruddy Turnstone	Spring migration	10.3	91.2	7.6	103.0	15.4	88.7

and in the post-arrival phase at Alert, Canada, found that the earliest arriving birds carried substantial stores of fat and protein, but that these were lost rapidly after arrival. Arriving Red Knots carried on average 42 g fat, much higher than the 16 g observed in our study. Semipalmated *Calidris pusilla* and White-rumped Sandpipers *Calidris fuscicollis* arrived in the southernmost part of their breeding ranges near Churchill, Manitoba, with average fat indices of 12.5 and 13.5% (calculated from Krapu et al. 2006). These two species depart from North Dakota with fat indices of 22.0 and 24.5%, respectively. Little Stints are similar in size to Semipalmated Sandpipers, but arrived with a lower mean fat index (6.6%). Sanderling and Dunlin are slightly larger than White-rumped Sandpiper and also arrive with lower fat indices (9.4 and 10.0%). These differences might be due to the fact that the American species were caught at the very southern edge of (or for White-rumped Sandpiper, even 400 km south of) the breeding range.

Function of nutrient stores upon arrival: survival insurance for a snow-covered tundra?

A possible function of arrival stores could be insurance in case feeding is not yet possible upon arrival owing to snow cover. The average fat stores with which the birds arrived varied between 1.6 g for Little Stint and 16.1 g for Red Knot (Table 2). Assuming a daily energy expenditure (DEE) of 2.3 times basal metabolic rate (BMR) (Wiersma and Piersma 1994), using published BMR values (Lindström and Klaassen 2003) and an energetic equivalent of 39 kJ per g fat (Ricklefs 1974), these fat stores could sustain fasting birds for 0.8 (Little Stint) to 2.8 days (Red Knot) if forced to fast (Table 4). These survival periods are positively related to mean arrival body mass among species ($F_{1,6} = 11.99, P = 0.017$). The maximum fat stores measured enabled a range of survival times from 1.7 days in Sanderling (minimum) to 4.4 days in Red Knot (maximum, Table 4). In addition to fat stores, part of the protein

Table 4 Estimated survival times based on arrival fat stores (Table 2, published Basal Metabolic Rate (BMR) values (Lindström and Klaassen 2003), the assumption of a daily energy expenditure (DEE) of 2.3 BMR (Wiersma and Piersma 1994) and an energetic equivalent of 39 kJ/g fat (Newton 2008)

Species	Body mass (g)	Fat mass (g)				DEE (kJ) (2.3 BMR)	Survival (<i>n</i> days)		
		Mean	Min	Max	BMR		<i>n</i> days	Min	Max
Dotterel	121.4	6.3	5.0	12.3	1.1	221.9	1.1	0.9	2.2
Red Knot	126.0	14.5	8.1	25.7	1.1	227.9	2.5	1.4	4.4
Sanderling	48.5	3.5	3.7	4.6	0.5	105.3	1.3	1.4	1.7
Little Stint	25.3	1.2	0.0	5.2	0.4	73.5	0.6	0.0	2.8
Curlew Sandpiper	59.0	4.6	-0.2	11.5	0.6	121.2	1.5	0.0	3.7
Dunlin	48.4	3.8	0.4	6.4	0.6	119.2	1.2	0.1	2.1
Turnstone	102.9	10.3	3.6	19.5	0.9	186.8	2.2	0.8	4.1

reserves in the body (lean mass) are also metabolised before birds starve to death (Jenni-Eiermann and Jenni 1996; Groscolas and Robin 2001). Because of the lower energy content of protein, these reserves will contribute less to survival time than fat stores, but limited stores in the range measured in our study could provide some leeway if conditions upon arrival prevent feeding, or at least give time to look for nearby sites where spring is more advanced.

Function of nutrient stores upon arrival: rebuilding organs?

Upon arrival organs that are reduced prior to the migratory journey, specifically digestive organs, need to be rebuilt. Morrison et al. (2005, and see Morrison 2006) concluded that in Red Knots metabolites that become available from arrival stores are used to enable body changes including an increase in mass of digestive organs. For three of the four species tested in our study (Little Stint, Dunlin and Curlew Sandpiper), arrival body mass was lower than that during incubation (Table 1), while fat indices were higher in arriving than in incubating Dunlin and Little Stint (Table 2). In Little Stints this was not due to lower fat mass but to an increase in lean mass during incubation; in Dunlin this was caused by both a decrease in fat mass and an increase in lean mass. The increase in lean mass may indicate that nutrient stores upon arrival were used to rebuild organs, but as total body mass increased it is also clear that exogenous nutrients, collected after arrival on the breeding grounds, must make a contribution.

Function of nutrient stores upon arrival: used for egg formation?

In the pre-breeding phase shorebirds need to acquire energy not only for egg formation, but also to remain in good condition to make it through the time- and energy-demanding incubation period (Piersma et al. 2003). Small shorebirds, particularly those in which one adult incubates alone (e.g. Little Stint and Curlew Sandpiper) need stores to endure bad weather periods during breeding (Tulp et al. 2002; Tulp and Schekkerman 2006). Arrival with some stores remaining can give them a head start.

If arrival stores play a role in egg formation, we expect females to arrive with greater stores than males (Sandberg and Moore 1996; Smith and Moore 2003). In Dunlin, Curlew Sandpiper and Ruddy Turnstones, females were significantly heavier in the arrival period than males, but body mass did not differ between the sexes in Red Phalarope (although sample size was very low). However, these sex differences could not be distinguished from a size effect (structural size measures were interchangeable with sex in the analyses). If in any species, a sex difference would be expected in Red

Phalarope, since the females defend the territories, have to court a male and produce the eggs. For Curlew Sandpiper, the only species for which enough TBW measurements were carried out on both sexes in the arrival period, we did not find a significant difference in either fat stores or lean mass in the arrival period after correction for structural size. Similarly Morrison (2006) did not record differences in fat store between the sexes in Red Knots. The absence of sex differences in arrival stores could also be caused by the fact that although females need additional energy for egg formation, males need substantial energy to establish and maintain a territory, as well as to court a female.

Based on our data we cannot rule out the possibility that females bring specific nutrients to the breeding area (necessary for egg formation or organ build-up), that are not reflected in a difference in mass of body stores. Morrison and Hobson (2004) and Klaassen et al. (2001) however, have shown that eggs of Red Knots and other shorebird species consist primarily of local terrestrial nutrients and only the earliest laid eggs showed some possible contribution of marine nutrients originating from non-breeding sites. Stores still present upon arrival are therefore likely not to be used for egg production but for rebuilding organs and as an insurance against bad food conditions upon arrival. However, these studies have been carried out in the Nearctic only. Given the different geographical setting of the migration routes, comparable studies on the Palearctic tundra are called for.

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