High daily energy expenditure of incubating shorebirds on High Arctic tundra: a circumpolar study

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Summary

1. Given the allometric scaling of thermoregulatory capacity in birds, and the cold and exposed Arctic environment, it was predicted that Arctic-breeding shorebirds should incur high costs during incubation. Using doubly labelled water (DLW), daily energy expenditure (DEE) during incubation was measured in eight shorebird species weighing between 29 and 142 g at various sites in the Eurasian and Canadian High Arctic. The results are compared with a compilation of similar data for birds at lower latitudes.
2. There was a significant positive correlation between species average DEE and body mass (DEE (kJ day^{-1}) = 28·12 BM (g)$^{0·524}$, r^2 = 0·90). The slopes of the allometric regression lines for DEE on body mass of tundra-breeding birds and lower latitude species (a sample mostly of passerines but including several shorebirds) are similar (0·548 *vs* 0·545). DEE is about 50% higher in birds on the tundra than in temperate breeding areas.
3. Data for radiomarked Red Knots for which the time budgets during DLW measurements were known, indicated that foraging away from the nest on open tundra is almost twice as costly as incubating a four-egg clutch.
4. During the incubation phase in the High Arctic, tundra-breeding shorebirds appear to incur among the highest DEE levels of any time of the year. The rates of energy expenditure measured here are among the highest reported in the literature so far, reaching inferred ceilings of sustainable energy turnover rates.

Key-words: Allometry, body size, doubly labelled water, energy budget, field metabolic rate

Functional Ecology (2003) **17**, 356–362

Introduction

Some shorebird species travel thousands of kilometres each year to breed in one of the coldest regions in the world, the High Arctic. Although shorebirds breed during the local summer season, their nests are open and poorly insulated (Andreev 1999). As a consequence of the thermoregulatory demands of the weather, and the high costs of warming the eggs, we predict that tundra-breeding shorebirds have high daily energy expenditures. Indeed, the two studies to date that provide measurements of daily energy expenditure (DEE) of free-living shorebirds during the incubation phase on High Arctic tundra (Piersma & Morrison 1994; Morrison, Davidson & Piersma 1997; in both cases Ruddy Turnstones *Arenaria interpres*), concluded that their expenditure approached, and sometimes exceeded, the suggested maximum for high levels of energy expenditure, the so-called 'metabolic ceiling' k_{max} (Drent & Daan 1980; Kirkwood 1983; Hammond & Diamond 1997; Piersma 2002).

We measured DEE in eight species of shorebirds with a five-fold range in body mass (29–142 g) at places distributed over much of the circumpolar tundra. These data are compared with similar measurements

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of other species during incubation at lower latitudes. All studies employed the doubly labelled water (DLW) technique (Speakman 1997). We briefly explore whether intraspecific variation in daily energy expenditure might be the result of expenditure during actual incubation (Andreev 1999), or rather due to high costs of thermoregulation when the birds take a foraging recess (Wiersma & Piersma 1994; Cartar & Morrison 1997).

Study sites and methods

STUDY SITES

Data were collected during four separate expeditions in the Eurasian and Canadian Arctic during the summers of 1994 and 1999 (Appendix 1).

1. During the ship-based Swedish–Russian Tundra Ecology-Expedition-94 (Grönlund & Melander 1995), scientists were put ashore with helicopters for 24–48 h at relatively nearshore sites in the Eurasian Arctic. DEE data were collected at three different sites: 12–13 June 1994 on north-east Kanin Peninsula (67° N, 41° E, site A), 14–15 June on Kolguyev Island (69° N, 50° E, site B) and 18–20 June on the western Yamal Peninsula (70° N, 67° E, site C).
2. The Dutch–Russian 'Knots at Sterlegova'-expedition took place from 10 June to 12 August 1994 at Cape Sterlegov in northern Taimyr (75°25′ N, 89°08′ E, site D), and DLW measurements were made of shorebirds with a known nesting record (Tulp *et al.* 1998).
3. The Swedish Tundra North-west-99 expedition was based on a Canadian icebreaker (Grönlund 2000), and visited a series of stations along the North-west Passage. At two of these sites, in Cresswell Bay on Somerset Island (72°55′ N, 93°27′ W, site E) and on the Graham Gore Peninsula of King William Island (69°07′ N, 98°55′ W, site F), we were able to make measurements on incubating individuals within the 24–36-h periods ashore.
4. The Canadian Wildlife Service has maintained research activities on northern Ellesmere Island, based at the Canadian Forces Station Alert (82°30′ N, 62°19′ N, site G) since 1974 (Morrison 1975; Morrison & Davidson 1990). Studies of incubating Ruddy Turnstones were made in July 1994 (published in Morrison *et al.* 1997), and of an incubating Sanderling in July 1999.

In addition to results of these four research projects, the data for Ruddy Turnstones collected in June–July 1989 at Rowley Island, Foxe Basin (68°56′ N, 79°18′ W) and published by Piersma & Morrison (1994) were incorporated here.

Despite their wide geographical spread, ranging from 67 to 82° N, and from 99° W to 89° E, the physiognomy of the study sites was quite comparable. They were all sparsely vegetated with sedges, mosses and lichens, as is typical of tundra regions at the highest latitudes.

FIELD PROTOCOL

Most of the nests of birds studied here contained the standard shorebird clutch of four eggs (in a few cases three eggs) and given the general patterns of timing of breeding in the regions, were in mid- or late (i.e. the second or the third week of) incubation. Incubating birds were captured either by walk-in traps, a self-triggered Russian-designed clapnet (*lukchok*), a small pull-trap (Hicklin, Hounsell & Finney 1989), or by depositing a mistnet over bird and nest. Upon capture, birds were weighed to the nearest gram. A blood sample was taken from the brachial vein to establish background values of the stable isotopes at each study site (these values were always slightly lower than those for the Vienna Standard Mean Ocean Water). Then the birds received a subcutaneous injection in the pectoral area of a known volume of doubly labelled water. Before injection, the water had been warmed up to human skin temperature by skin contact. The DLW dose ranged from a low 2.6 mg g^{-1} for Ringed Plover *Charadrius hiaticula* to a high of 5.5 mg g^{-1} for Little Stint *Calidris minuta*. For the experiments reported here we used three different DLW mixtures (one at locations A–D, another at locations E and F, and a third mixture at Rowley Island in 1989).

Following administration, the birds were kept in a cloth bag for about an hour to allow equilibration with the bird's body water pool (Speakman 1997). During this time incubation duties were often taken over by the partner, but in cold weather and the obvious absence of the partner the eggs were prevented from rapid cooling by covering them with a glove containing warming sticks. During the hour that birds were kept, we applied metal and colour rings, and measured body dimensions. Just before release, an additional series of three to six blood samples was collected. Each capillary contained about 10–30 µl blood and was flame-sealed. Blood samples were stored in cool dark conditions for up to 6 months before analysis. After release birds either returned to their nest to resume incubation within a few minutes (the usual procedure with Red Knots and Sanderlings) or, when the partner had taken over incubation duty, went off to bathe and preen. In the majority of cases, regular checks were made at the nest throughout the period of measurement to see whether birds continued their normal routine. In none of the cases presented did we have reason to believe that daily activity patterns were much disturbed. Data establishing this are presented below for the largest shorebird species (Red Knot). In a follow-up study on the smallest species, Little Stint, using temperature-loggers in the nest it could be demonstrated that DLW-injected birds readily returned to the nest (I. Tulp & H. Schekkerman, unpublished data).

After approximately a day (or an interval determined by the presence/absence on the nest of the focal bird in the case of radiotagged Red Knots; see below), we recaptured the individuals using one of several catching methods, usually one that was different from the ones used earlier. Again three to six capillaries of blood were collected and flame-sealed after which the bird was weighed and released. Some Red Knots were recaptured and bled several times in succession (see below).

At Cape Sterlegov (site D) all Red Knots loaded with DLW were fitted with 1·8 g radiotransmitters (Holohil, Carp, Canada, BD-2G transmitters, 173·199–173·350 Hz) and followed around the clock. Birds were radiotagged 1–3 days before injection, and then followed throughout and beyond the period of measurement of DEE. As we quantified the presence or absence on the nest of individuals at hourly intervals, we were able to precisely time capture and thus subsequent injection of DLW and (repeated) blood sampling. Thus we could adjust measurement periods to cover only a period of incubation, a period of foraging, or both. The radio-based observations also showed that the DLW measurements had no discernible effect on incubation schedules. The attachment of a small radiotag in principle could have affected the insulation properties of a tagged bird. As we were unable to obtain DLW measurements of untagged Red Knots, we cannot properly evaluate such an effect on DEE. However, given that the radiotags were always completely covered with the feathers of the back and the wings, and were thus invisible except for a few cm of antenna extending beyond the tail, we believe that any such effect is minimal. As the radiotags contributed less than 1·5% extra mass, we expect the extra mass to have little influence on energy demand.

For practical reasons it was not possible to collect the appropriate weather data for measuring operative temperatures consistently and systematically (Wiersma & Piersma 1994; Cartar & Morrison 1997) during each of the DLW measurements, although good local weather data were available for the key sites (e.g. Cape Sterlegov, Tulp *et al.* 1998). Average air temperatures during DLW measurements were always between 0 °C and 9 °C. Using the part of the data set that was complete, we were unable to explain any of the remaining variance in rates of energy expenditure once body size effects were accounted for.

ISOTOPE ANALYSES AND CALCULATIONS

On the basis of gravimetric determinations of the quantities of ^2H_2O and $H_2^{18}O$ used for the preparations, as well as their known enrichments (supplier's values) concentrations of the isotope mixture were calculated and verified by employing a dilution experiment with distilled water with known ^2H and ^{18}O enrichments. The determinations of the $^2H/^1H$ and $^{18}O/^{16}O$ isotope ratios of the blood samples were performed at the

Centre for Isotope Research employing procedures described by Visser & Schekkerman (1999). With each batch of shorebird samples, a minimum of three internal laboratory water standards with different enrichments (stored in flame-sealed capillaries and calibrated against IAEA standards) were analysed four times. All isotope analyses were run in duplicate, and two additional capillaries were analysed if the duplicates differed by more than 2·5%.

For each site and most species, one to four samples were taken prior to injection of the isotope mixture, to assess the species-specific background concentrations (C_{back}) of ^2H and ^{18}O. The quantitative injection of the isotope mixture (M_{inj}; mol), its known ^{18}O concentration (C_{inj}), and the ^{18}O concentration of the initial sample (C_{init}), enabled an individual-specific determination of the total amount of body water (TBW, g):

$$\text{TBW} = 18 \cdot 02 \times M_{inj}(C_{inj} - C_{init})/(C_{init} - C_{back}). \quad \text{eqn 1}$$

For each trial, the rate of CO_2 production (moles day^{-1}) was calculated using Speakman's (1997) equation:

$$r\text{CO}_2 = N/2 \cdot 078(k_o - k_{Da}) - 0 \cdot 0062 \times N \times k_{Da}, \quad \text{eqn 2}$$

where N represents the size of the body water pool (moles), k_o (day^{-1}) and k_{Da} (day^{-1}) represent the fractional turnover rates of ^{18}O and ^2H, respectively, which were calculated using the species-specific background concentrations and the initial and final ^{18}O and ^2H concentrations (Lifson & McClintock 1966). The equation used is a modification of equation #35 listed in Lifson & McClintock (1966). The equation we used takes fractionation effects of molecules with heavy isotopes into account under the assumption that 25% of the water efflux is lost through evaporative pathways. This estimate is probably more realistic than the value of 50% employed by Lifson & McClintock (1966; for discussion see Verboven & Piersma 1995; Speakman 1997; and Visser & Schekkerman 1999). Finally, the rate of CO_2 production was converted to energy expenditure assuming a molar volume of 22·4 l mol^{-1} and an energetic equivalent of 27·33 kJ l^{-1} CO_2, based on an insectivorous diet (on the tundra, shorebirds eat mainly insects and some spiders; T. Piersma *et al.*, personal observation) (Gessaman & Nagy 1988). For each trial, the water efflux rate was calculated using the equation of Nagy & Costa (1980), under the assumption that 25% of the water efflux rate was lost through evaporative pathways (see above).

In addition to the DEE values discussed in this paper we also present our estimates of total body water (as a percentage of body mass), and of water influx and efflux (Appendix 1). In accordance with almost all published studies, values for DEE are presented with day as the time unit (i.e. kJ day^{-1}). However, again in accordance with common usage, the costs of specific activities such as incubation or foraging are expressed in W (1 W = 86·4 kJ day^{-1}).

Table 1. Average daily energy expenditure during the incubation phase in eight arctic-breeding shorebird species, as measured by doubly labelled water. For Ruddy Turnstone, data from Piersma & Morrison (1994; $n = 8$) and Morrison *et al.* (1997; $n = 3$) have been included

Species	n	Body mass (g)	SD	DEE (kJ day^{-1})	SD
Little Stint	3	29	0·8	184·8	17·1
White-rumped Sandpiper	1	39		189·6	
Dunlin	7	53	2·0	192·7	36·9
Ringed Plover	3	57	5·6	218·8	16·1
Sanderling	4	59	2·5	229·2	30·9
Purple Sandpiper	1	79		307·7	
Ruddy Turnstone	16	108	6·0	348·1	59·2
Red Knot	6	142	9·9	373·5	31·4

COMPARATIVE DATA AND STATISTICS

A data set based on DLW measurements for terrestrial birds (including shorebirds) during the incubation phase at lower latitudes has recently been compiled by Tinbergen & Williams (2002). We have relied on their review for comparative purposes.

Statistics were carried out in SPSS 8·0 and SYSTAT. For comparisons between species, ANCOVA and linear regressions were made after log$_{10}$-transforming DEE and body mass values. For intraspecific comparisons, data were not transformed.

Results and discussion

DEE during the incubation phase was measured in 30 individuals of eight shorebird species (1–7 individuals per species; Appendix 1). Data for two Long-tailed Skuas *Stercorarius longicaudus* are also presented. The average values for body mass (g) and DEE (kJ day^{-1}) for the shorebird species are given in Table 1. For the Ruddy Turnstone, the data originate from three sites: D, G and Rowley Island (Piersma & Morrison 1994; Morrison *et al.* 1997). There were no significant differences in either body mass or DEE between these three sites (ANOVA, body mass, $F_{2,13} = 0·76$, $P = 0·50$; DEE, $F_{2,13} = 0·07$, $P = 0·93$).

Within the set of eight species of Arctic-breeding shorebirds there was a significant positive correlation between species-average DEE and body mass (Table 1): DEE (kJ day^{-1}) $= 28·12$ BM (g)$^{0·524}$ ($r^2 = 0·90$, $P < 0·001$, SE of slope 0·072).

Note that the data point of the single plover species is indistinguishable from the sandpiper values. Note also that data points based on small n-values (Table 1) are not outliers. When we include the average for Long-tailed Skua, the relationship is only slightly changed to DEE (kJ day^{-1}) $= 25·59$ BM (g)$^{0·548}$ ($r^2 = 0·96$, $P < 0·001$, SE of slope 0·044).

In most of the species and studied pairs, males and females shared incubation duties. In the two smallest species, Little Stint and White-rumped Sandpiper *Calidris fuscicollis*, only one of the partners incubated. The average DEE of Little Stints from Cape Sterlegov on Taimyr Peninsula was relatively the highest, and
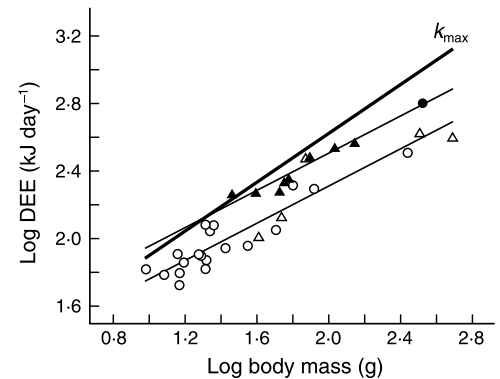

Fig. 1. Daily energy expenditure as a function of body mass in tundra-breeding species (closed symbols) during the incubation phase compared with DEE of lower latitude bird species (open symbols; from Tinbergen & Williams 2002). Shorebirds of the families Charadriidae (*Charadrius alexandrinus, Ch. hiaticula*), Recurvirostridae (*Recurvirostra avosetta*), Haematopodidae (*Haematopus ostralegus*) and Scolopacidae (*Actitis hypoleucos, Calidris* sp., *Arenaria interpres*), are indicated with triangles, the other species with circles. k_{max} is the suggested absolute upper limit to daily metabolizable energy intake to be found in homeotherm animals (Kirkwood 1983).

was the only measured DEE that exceeded predicted k_{max} (Fig. 1). However, the data point for White-rumped Sandpiper was precisely as expected on the basis of body size.

Based on the data for radiomarked Red Knots at Cape Sterlegov (site D), it was possible to investigate whether the field metabolic rate is a function of the type of activity (incubating, foraging away from the nest, or both; Fig. 2). Although there were no significant differences in body mass between the three categories (ANOVA, $F_{2,6} = 0·05$, $P = 0·954$) and no differences in average air temperatures during the periods of DLW-measurement ($F_{2,6} = 2·25$, $P = 0·187$), there were significant differences between the field metabolic rates of the activity categories (ANOVA, $F_{2,6} = 15·2$, $P = 0·004$). *Post hoc* Scheffe tests assuming independent data points showed that all pairwise differences between categories were significant ($0·005 < P < 0·046$). For the particular bird in which each activity category was covered by a DLW measurement (female #7), foraging
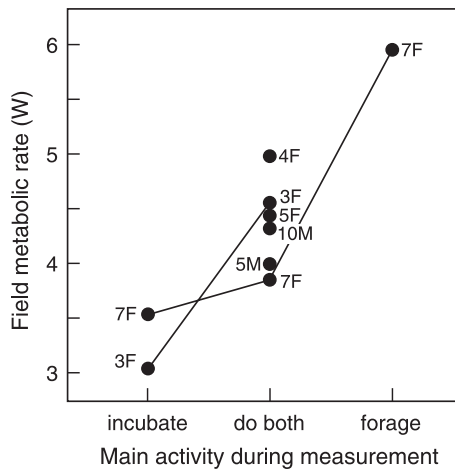
Fig. 2. Field metabolic rate of red knots as a function of their main activity during periods of DLW measurement during the incubation phase at Cape Sterlegov, Taimyr Peninsula in July 1994 (see Appendix 1 for overall values for the different individuals). Note that we were unable to collect detailed activity budgets and thus unable to calculate activity-specific costs.

on the tundra was 1·8 times more costly than incubating a clutch.

Shorebirds breeding on the tundra have a significantly higher DEE than the birds breeding at more southern latitudes (ANOVA, $F_{1,30} = 30\cdot6$, $P < 0\cdot001$; Fig. 1), but the exponents do not differ between the groups (interaction term $P > 0\cdot9$). Indeed, they are almost identical (0·548 *vs* 0·545). Over the entire body size-range, measured DEE is about 50% higher in birds breeding on the tundra than at temperate latitudes (Tinbergen & Williams 2002). Five of the 24 data points from the temperate zone were from shorebirds (18 were from passerines, birds with similarly high basal metabolic rates as shorebirds, e.g. Kersten & Piersma 1987), and these data generally confirmed that our values for DEE were high because of High Arctic conditions, not because the data represent shorebirds (see also Schekkerman *et al.* 2003 for similar findings for growing shorebird chicks). For example, Amat *et al.* (2000) had DEE-values for incubating Kentish Plovers *Charadrius alexandrinus* from southern Spain. This small plover (with an average body mass of 40·9 g), exhibited a DEE level of 103·9 kJ day⁻¹ (SD = 19·7, n = 15), which is 46% lower than the value of 193 kJ day⁻¹ predicted on the basis of the equation for High Arctic breeding birds. At the high end of the mass-scale for comparisons are measurements of DEE of 435 kJ day⁻¹ in 325-g Avocets *Recurvirostra avosetta* (Hötker, Kölsch & Visser 1996) and of 500 kJ day⁻¹ in 533-g Oystercatchers *Haematopus ostralegus* (Kersten 1996). These values are, respectively, 27% and 36% less than predicted for Arctic breeding birds. The two remaining temperate-breeding shorebird values are for Common Sandpiper *Actitis hypoleucos* and Ringed Plover, respectively (Tatner & Bryant 1993). The latter estimate, based on four data-points, is very high, even

higher than our average for the same species in the High Arctic. This difference is puzzling and can be explained only if the sampled plovers spent most of their time on energetically costly activities off the nest between release and recapture. However, no activity data were collected (D. M. Bryant, personal communication).

The DEE of the Arctic shorebirds in our study were all close to the 'metabolic ceiling' deduced on the basis of maximum daily metabolizable energy intake rates in homeotherms (Fig. 1) (Kirkwood 1983). Castro, Myers & Ricklefs (1992) measured DEE of wintering Sanderlings at different latitudes and found the highest values at the coldest wintering sites. Our data for breeding Sanderlings exceed these values. Thus, DEE levels of incubating tundra-breeding shorebirds are among the highest in the annual cycle (Drent & Piersma 1990; Piersma 2002).

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Appendix 1

Daily energy expenditure during the incubation phase of individual birds, as measured with the doubly labelled water method. Species were arranged according to body mass. The studies were carried out in 1994 (sites A–D) and 1999 (sites E–G). Body mass is the average mass over the measurement period

Species	ID[a]	Site[b]	Start of experiment[c]	Duration (h)	Body mass (g)[d]	DLW measurements: water			
						DEE (kJ day^{-1})	TBW (%)	H_2O_{out} (g day^{-1})	H_2O_{in} (g day^{-1})
Little Stint	#01	D	09 July (16, 38)	21·4	30·2	181·8	63·3	43·7	42·1
Little Stint	#04	D	16 July (13, 16)	24·2	29·0	203·2	72·2	34·2	34·2
Little Stint	#10	D	26 July (15, 37)	22·9	28·8	169·4	71·9	33·6	34·5
White-rumped Sandpiper	#01	E	09 July (22, 01)	20·9	39·0	189·6	68·3	33·5	32·0
Dunlin	#02	B	14 June (15, 09)	24·1	51·8	192·4	69·2	71·2	72·3
Dunlin	#03	B	14 June (14, 48)	27·9	51·3	184·1	69·6	77·5	77·2
Dunlin	#04	B	14 June (15, 40)	23·9	50·8	165·3	66·3	57·0	56·0
Dunlin	#05	B	14 June (16, 08)	23·2	54·0	149·7	68·7	56·7	54·6
Dunlin	#06	B	14 June (16, 44)	23·6	50·3	226·4	68·7	66·7	67·8
Dunlin	#08	B	14 June (20, 41)	21·1	53·5	175·0	70·4	59·3	58·5
Dunlin	#10	C	19 June (21, 26)	14·7	55·8	256·4	68·0	46·1	44·4
Ringed Plover	#01	A	12 June (19, 35)	21·3	52·5	215·9	64·8	59·1	57·7
Ringed Plover	#1F	D	3 July (19, 08)	23·0	63·0	236·2	64·4	45·4	44·1
Ringed Plover	#1M	D	3 July (18, 32)	23·0	54·5	204·3	65·1	45·0	44·3
Sanderling	#D2	D	20 July (20, 50)	36·2	62·3	244·9	59·5	23·9	20·0
Sanderling	#A1	E	10 July (01, 20)	21·2	57·0	214·5	62·8	26·3	26·3
Sanderling	#A2	F	20 July (12, 15)	23·6	57·0	263·4	68·6	61·5	61·5
Sanderling	#01	G	9 July (16, 50)	47·7	58·5	194·0	59·1	32·0	31·1
Purple Sandpiper	#X1	D	15 July (12, 45)	22·3	79·0	307·7	63·1	74·3	73·0
Ruddy Turnstone	#2F	D	6 July (19, 02)	43·2	102·8	361·9	63·8	80·0	79·0
Ruddy Turnstone	#9F	D	2 July (16, 20)	24·4	107·0	311·4	66·0	70·3	70·3
Ruddy Turnstone	#9M	D	2 July (17, 18)	29·6	102·5	332·1	65·8	51·4	48·7
Ruddy Turnstone	#10M	D	1 July (22, 58)	34·1	110·5	342·7	66·7	66·6	64·3
Ruddy Turnstone	#13F	D	7 July (19, 33)	45·6	107·0	350·1	60·3	51·6	49·7
Red Knot	#3F	D	7 July (18, 31)	40·0	142·5	344·6	61·5	65·0	62·1
Red Knot	#4F	D	8 July (16, 45)	56·5	141·6	429·9	67·3	114·9	116·4
Red Knot	#5F	D	9 July (19, 17)	40·0	159·5	381·6	59·3	70·8	67·6
Red Knot	#5M	D	30 June (13, 10)	27·3	129·5	345·1	65·2	55·9	50·7
Red Knot	#7F	D	8 July (18, 43)	55·4	142·0	366·5	63·5	76·8	75·8
Red Knot	#10M	D	9 July (19, 07)	21·4	137·0	373·2	58·5	94·3	95·6
Long-tailed Skua	#1F	D	2 July (00, 38)	22·7	378·5	686·9	59·3	92·2	71·4
Long-tailed Skua	#1M	D	2 July (01, 02)	21·7	293·5	583·0	58·8	73·4	68·8

[a]The addition of an M means that the individual was identified as a male, and with an F as a female.

[b]Letters refer to the following study sites: A = north-east Kanin Peninsula, B = Kolguyev Island, C = western Yamal Peninsula, D = Sterlegov Cape on Taimyr Peninsula, and E = Somerset Island, F = King William Island, and G = Alert.

[c]Day and month (h, min).

[d]The body mass presented here is the average of body mass upon release and (final) recapture, as covered by the indicated duration of the DLW experiment in the previous column.