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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

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’ \(k_{\text{max}}\) (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
of High Arctic shorebirds

Energy expenditure

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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.

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 Kolguiev 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 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 to high costs of thermoregulation when the birds take a foraging recess (Wiersma & Piersma 1994; Cartar & Morrison 1997).
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 $^{2}$H$_{2}$O 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 $^{2}$H and $^{18}$O enrichments. The determinations of the $^{2}$H/^{1}$H$ 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$_{bck}$) of $^{2}$H 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$_{init}$), allowed an individual-specific determination of the total amount of body water (TBW, g):

\[TBW = 18.02 \times M_{inj}(C_{inj} - C_{init})(C_{init} - C_{bck}) \]  

For each trial, the rate of CO$_{2}$ production (moles day$^{-1}$) was calculated using Speakman’s (1997) equation:

\[rCO_{2} = N/2 \times 0.0062 \times N \times k_{Da} \]  

where $N$ represents the size of the body water pool (moles), $k_{a}$ (day$^{-1}$) and $k_{Da}$ (day$^{-1}$) represent the fractional turnover rates of $^{18}$O and $^{2}$H, respectively, which were calculated using the species-specific background concentrations and the initial and final $^{18}$O and $^{2}$H 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>( n )</th>
<th>Body mass (g)</th>
<th>SD</th>
<th>DEE (kJ day(^{-1}))</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little Stint</td>
<td>3</td>
<td>29</td>
<td>0.8</td>
<td>184.8</td>
<td>17.1</td>
</tr>
<tr>
<td>White-rumped Sandpiper</td>
<td>1</td>
<td>39</td>
<td></td>
<td>189.6</td>
<td></td>
</tr>
<tr>
<td>Dunlin</td>
<td>7</td>
<td>53</td>
<td>2.0</td>
<td>192.7</td>
<td>36.9</td>
</tr>
<tr>
<td>Ringed Plover</td>
<td>3</td>
<td>57</td>
<td>5.6</td>
<td>218.8</td>
<td>16.1</td>
</tr>
<tr>
<td>Sanderling</td>
<td>4</td>
<td>59</td>
<td>2.5</td>
<td>229.2</td>
<td>30.9</td>
</tr>
<tr>
<td>Purple Sandpiper</td>
<td>1</td>
<td>79</td>
<td></td>
<td>307.7</td>
<td></td>
</tr>
<tr>
<td>Ruddy Turnstone</td>
<td>16</td>
<td>108</td>
<td>6.0</td>
<td>348.1</td>
<td>59.2</td>
</tr>
<tr>
<td>Red Knot</td>
<td>6</td>
<td>142</td>
<td>9.9</td>
<td>373.5</td>
<td>31.4</td>
</tr>
</tbody>
</table>

**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 fuscicolis*, only one of the partners incubated. The average DEE of Little Stints from Cape Sterlegov on Taimyr Peninsula was relatively the highest, and was the only measured DEE that exceeded predicted \( k_{\text{max}} \) (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...
Shorebirds breeding on the tundra have a significantly higher DEE than the birds breeding at more southern latitudes (ANOVA, $F_{1,30} = 30.6, P < 0.001$; Fig. 1), but the exponents do not differ between the groups (interaction term $P > 0.9$). 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 (Tattner & 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).

**Acknowledgements**

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**References**


Energy expenditure of High Arctic shorebirds


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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.

<table>
<thead>
<tr>
<th>Species</th>
<th>ID</th>
<th>Site</th>
<th>Start of experiment</th>
<th>Duration (h)</th>
<th>Body mass (g)</th>
<th>DEE (kJ day(^{-1}))</th>
<th>TBW (%)</th>
<th>(\text{H}<em>2\text{O}</em>{\text{out}}) (g day(^{-1}))</th>
<th>(\text{H}<em>2\text{O}</em>{\text{in}}) (g day(^{-1}))</th>
<th>(\text{H}<em>2\text{O}</em>{\text{in}}) (g day(^{-1}))</th>
</tr>
</thead>
<tbody>
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<td>Little Stint</td>
<td>#01</td>
<td>D</td>
<td>09 July (16, 38)</td>
<td>21.4</td>
<td>30.2</td>
<td>181.8</td>
<td>63.3</td>
<td>43.7</td>
<td>42.1</td>
<td></td>
</tr>
<tr>
<td>Little Stint</td>
<td>#04</td>
<td>D</td>
<td>16 July (13, 16)</td>
<td>24.2</td>
<td>29.0</td>
<td>203.2</td>
<td>72.2</td>
<td>34.2</td>
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<tr>
<td>Little Stint</td>
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<td>D</td>
<td>26 July (15, 37)</td>
<td>22.9</td>
<td>28.8</td>
<td>169.4</td>
<td>71.9</td>
<td>33.6</td>
<td>34.5</td>
<td></td>
</tr>
<tr>
<td>White-rumped Sandpiper</td>
<td>#01</td>
<td>E</td>
<td>09 July (22, 01)</td>
<td>20.9</td>
<td>39.0</td>
<td>189.6</td>
<td>68.3</td>
<td>33.5</td>
<td>32.0</td>
<td></td>
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<tr>
<td>Dunlin</td>
<td>#02</td>
<td>B</td>
<td>14 June (15, 09)</td>
<td>24.1</td>
<td>51.8</td>
<td>192.4</td>
<td>69.2</td>
<td>71.2</td>
<td>72.3</td>
<td></td>
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<tr>
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<td>B</td>
<td>14 June (14, 48)</td>
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<td>77.5</td>
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<td>50.8</td>
<td>165.3</td>
<td>66.3</td>
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<td>56.0</td>
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<tr>
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<td>54.6</td>
<td></td>
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<td>B</td>
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<td>46.1</td>
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<td>215.9</td>
<td>64.8</td>
<td>59.1</td>
<td>57.7</td>
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<tr>
<td>Ringed Plover</td>
<td>#1F</td>
<td>D</td>
<td>3 July (19, 08)</td>
<td>23.0</td>
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<td>64.4</td>
<td>45.4</td>
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<tr>
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<td>3 July (18, 32)</td>
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<td>204.3</td>
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<td>244.9</td>
<td>59.5</td>
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<td>E</td>
<td>10 July (01, 20)</td>
<td>21.2</td>
<td>57.0</td>
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<td>62.8</td>
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<td>Sanderling</td>
<td>#A2</td>
<td>F</td>
<td>20 July (12, 15)</td>
<td>23.6</td>
<td>57.0</td>
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<td>Purple Sandpiper</td>
<td>#X1</td>
<td>D</td>
<td>15 July (12, 45)</td>
<td>22.3</td>
<td>79.0</td>
<td>307.7</td>
<td>63.1</td>
<td>74.3</td>
<td>73.0</td>
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</tr>
<tr>
<td>Ruddy Turnstone</td>
<td>#2F</td>
<td>D</td>
<td>6 July (19, 02)</td>
<td>43.2</td>
<td>102.8</td>
<td>361.9</td>
<td>63.8</td>
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<tr>
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<td>#9F</td>
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<td>2 July (16, 20)</td>
<td>24.4</td>
<td>107.0</td>
<td>311.4</td>
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<tr>
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<td>D</td>
<td>2 July (17, 18)</td>
<td>29.6</td>
<td>102.5</td>
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<td>D</td>
<td>1 July (22, 58)</td>
<td>34.1</td>
<td>110.5</td>
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<tr>
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<td>D</td>
<td>7 July (18, 31)</td>
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<td>141.6</td>
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<td>30 June (13, 10)</td>
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<tr>
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<td>D</td>
<td>8 July (18, 43)</td>
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<td>142.0</td>
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<td>D</td>
<td>9 July (19, 07)</td>
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<td>137.0</td>
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<td>Long-tailed Skua</td>
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<td>378.5</td>
<td>373.2</td>
<td>58.5</td>
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<td>Long-tailed Skua</td>
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<td>2 July (01, 02)</td>
<td>21.7</td>
<td>293.5</td>
<td>583.0</td>
<td>58.8</td>
<td>73.4</td>
<td>68.8</td>
<td></td>
</tr>
</tbody>
</table>

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

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

*Day and month (h, min).

*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.