Chapter 3
Eggs in the freezer: energetic consequences of nest design in tundra breeding shorebirds

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For birds breeding in the Arctic, incubation is costly, and due to an increasing surface to volume ratio, more so in the smaller species. Small arctic birds may therefore place their nests in more thermally favourable microhabitats or invest more in nest insulation than large species. To test this hypothesis we examined different characteristics of nests of six species of arctic breeding shorebirds.

All species preferred the thermally most favourable sites and in a higher proportion than would be expected on the basis of habitat availability. Site choice, however, did not differ between the species. Permafrost depth measured next to the nests decreased in course of the season at similar speeds that did not differ between species, but permafrost was deeper under nests of larger species than under nests of the smallest species. Nest cup depth was unrelated to body mass^{0.73} (used as a measure of energy metabolism), but nest scrape depth (nest cup without the lining) decreased with body mass.

Cup depth divided by diameter^2 was used as a measure of nest cup shape and showed that small species had narrow deep and large nests, while large species had wide shallow nests. The thickness of nest lining varied between 1.5 cm and 3 cm and decreased significantly with body mass^{0.73}. We used the quantitative relationships derived empirically by Reid et al. (2002) to reconstruct the effect of different nest properties on the egg cooling coefficient. The predicted effect of nest cup depth on heat loss to the permafrost did not differ between species, but the sheltering effect of nest cup depth against wind and the effects of lining depth and material on cooling coefficient did increase with body mass^{0.73}. The combined effects indicate that small species invest most in the insulation of their nests.
Introduction

Most birds build a nest to lay and incubate their eggs in. The possible functions of building a nest can be various (Hansell and Deeming 2002): it might simply serve to keep the eggs together and keep individual eggs from rolling away, thus reducing the risk that one or more eggs are not incubated properly. Alternatively the nest provides protection against predation (Møller 1987; Sanchez-Lafuente et al. 1998). A well hidden nest in a deep scrape, even with vegetation partly covering the nest, is likely to reduce predation risk, not only if the bird sits on the nest, but also in absence of the incubating bird.

Another reason for nest building is that with a lined nest scrape, birds are likely to substantially reduce the rate at which their clutches lose heat and it enables them to control humidity inside the nest (Hansell 2000; Ar and Sidis 2002). Heat conservation is particularly important in cold environments (Szentirmai et al. 2005). The insulative properties of nests can also reduce heat loss of the incubating adult bird (Buttemer et al. 1987). The regulation of egg temperatures can be energetically demanding for parent birds (Williams 1996). Energy is required to maintain the temperature of the eggs at an appropriate level to ensure embryo development and to rewarm clutches that cooled down during the parents’ absence (Williams 1996). In the Arctic where daily energy expenditure is elevated because of the cold environment, incubation is costly, especially for small shorebirds (Tinbergen and Williams 2002; Piersma et al. 2003; chapter 6). Selection should therefore favour nest designs that reduce the rate of heat loss as much as possible in the light of other factors such as nest predation risks (Byrkjedal 1980; Whittingham et al. 2002). The majority of shorebirds (Charadrii) breed on the ground. They lay their eggs in nest cups varying from none at all (e.g. coursers), a shallow scrape without any nest lining (e.g. Kentish plover Charadrius alexandrinus), to rather deep and thickly lined scrapes (e.g. redshank Tringa tetanus, Cramp and Simmons 1983), sometimes hidden in thick vegetation but more often in more open sites such as grasslands and sparsely vegetated open ground (Piersma 1996a, b). Shorebirds generally lay pointed eggs. The position of the eggs oriented with their pointed ends towards the centre and downwards minimizes the amount of space needed to form the nest and increases the efficiency of the heat transfer from parent to egg. Most shorebird nests consist of scrapes that are made by one of the mates by pushing their breast towards the ground and scraping bottom surface material with their feet, using their breast to round the nest edges. The scrape is lined with a variety of materials including grass, moss, lichens or grit, forming a simple structure with a limited amount of lining material compared to nests of many other birds.

Many shorebird species breed in arctic regions, often nesting on open tundra just a few decimetres above the permafrost. Reid et al. (2002) experimentally showed for pectoral sandpipers Calidris melanotos that eggs placed in an excavated scrape and in a scrape with nest lining added, heat loss rates were reduced by 9% and 25%, respectively, in comparison with eggs placed on the tundra surface. This suggests that lined scrapes improve the insulation of clutches. They also showed that the insulative properties of a nest are determined by nest cup depth and shape, the thickness of the lining, and the type of lining material (Reid et al. 2002). Furthermore, ground temperature has been shown to have an important effect on heat loss to the ground (Cresswell et al. 2004). In nests of pectoral sandpiper that were experimentally heated, nest attendance increased, the effect being stronger when ground temperature was lower.

Piersma et al. (2003) showed that shorebirds incubating clutches in high arctic tundra have a Daily Energy Expenditure (DEE) that is about 50% higher than that of similarly sized
birds breeding in temperate areas. The allometric scaling exponent for DEE was 0.55, which is smaller than the scaling exponents for Basal Metabolism (0.73-0.71, Lasiewski and Dawson 1967; Kersten and Piersma 1987; Lindström and Klaassen 2003), and for maximum sustained levels of energy turnover in birds (0.72, Kirkwood 1983; Kvist and Lindström 2000). Consequently, DEE during incubation is likely to represent a larger challenge to the birds’ energy-processing capacity in small than in larger wader species, and small species will thus have most to gain by reducing heat loss from nests. We therefore hypothesise that within the same environment, small shorebirds should either place their nests in more thermally favourable microhabitats, or invest more in nest insulation than larger species. In addition to this body size effect, parental care system may play a role because species with uniparental incubation have less time available for foraging than species which share incubation duties between the sexes (chapters 4 & 6). A well-insulated nest may be important in these species to reduce egg cooling rates and increase the length of feeding absences.

Apart from insulative properties, predation risk may be an important factor in nest design and could limit size and depth of the nest. Large nests are likely to attract the attention of both visual (skuas, snowy owl Nyctea scandiaca) and olfactory hunting predators (e.g. arctic fox Alopex lagopus) more than small nests. To reduce predation risk, nests of arctic breeding shorebirds are extremely well camouflaged.

We tested the hypothesis that small species place their nests in more thermally favourable microhabitats and/or invest more in nest insulation than large species, by collecting data on nest location, nest cup size and shape, and thickness and composition of lining material in six shorebird species breeding sympatrically in the arctic tundra of western Taimyr, Siberia, Russia. We applied the quantitative relationships between nest properties and egg cooling coefficient derived for pectoral sandpiper nests by Reid et al. (2002) to estimate their relative effect in these six species, in isolation and in combination.

**Methods**

**Study area and species**

Data were collected during June-early August 2002 at Medusa Bay, in the west of the Taimyr Peninsula, Siberia (73°20’N, 80°30’E). The habitat consists of arctic tundra (Chernov 1985) and was characterised by rolling hills up to 50 m above sea level, and scattered stony ridges. Vegetation consisted of moss, lichen, grasses and tiny polar willows S. polaris generally not higher than 10 cm with a significant proportion of the soil surface bare. Sedge meadows with low Salix reptans shrubs occur in wet valleys and in flat places on the watersheds. Average summer temperature (2000-2002) and wind speed in the incubation period (ca 15 June-15 July) is 4.3°C and 7.1 m s⁻¹. See for a more detailed description (Schekkerman et al. 2004).

We collected data on nests of six shorebird species (ordered by increasing average mass during incubation as measured in the study area (Schekkerman et al. 2004): little stint Calidris minuta (30 g, N = 61 nests), red phalarope Phalaropus fulicarius (51 g, N = 6), dunlin C. alpina (54 g; N = 22), curlew sandpiper C. ferruginea (65 g; N = 12), ruddy turnstone Arenaria interpres (101.4 g; N = 9), and Pacific golden plover Pluvialis fulva (132.5 g, N = 18). Common ringed plover Charadrius hiaticula is also a common breeding bird in the area but was excluded from this study because it nests in a very different habitat (gravel plains and shingle banks along rivers) and did not have the same types of lining material available. Although the six species did show differences in their preferred nesting habitat within the vegetated tundra (with red phalarope, little stint and dunlin in or close to the wetter areas and curlew sandpiper, turnstone and Golden Plover on dryer parts), there was extensive overlap between
them and nests of different species were often found in close proximity. Incubation is uniparental in little stint, red phalarope and curlew sandpiper, and is shared between the sexes in the three other species (Hildén 1978; Cramp and Simmons 1983; Reynolds 1987; Tomkovich and Soloviev 2006).

**Nest measurements**

Shorebirds started laying eggs shortly after snow melt. Nests were located by intensive searching during and after the laying period. When a nest was found we categorised its general position: on horizontal ground either in lowlands or on watersheds, or on slopes facing roughly north, south, east or west. These positions were given a rank score with respect to thermal favourability on the basis of their exposure to sun (favourable) and wind (unfavourable). In northern Taimyr in summer, northern winds are generally cold since they arrive over the sea-ice and the Arctic Ocean; southern winds bring warmer air from the continent. Nest positions were ranked in decreasing order of favourability as 1 south slopes, 2 west and east slopes, 3 flat lowlands, 4 flat watersheds, and 5 north slopes. The proportional availability of tundra in each of these categories was estimated from maps of the study area.

Upon finding a nest we floated two eggs in water to estimate the time they had been incubated (Schekkerman et al. 2004; Liebezeit et al. 2007) and back calculated the laying date (of the last egg). We measured the depth of the permafrost next to the nest by pushing a metal pin into the substrate until it hit the ice (figure 3.1). Nests were marked using GPS and checked regularly. On at least one of these repeated visits permafrost depth was measured again. The change in depth of the permafrost underneath nests was described by linear regression on all measurements taking into account possible differences between species, and the results were used to estimate permafrost depth at laying for each nest.

The depth of the nest cup (cm) was measured by lowering a ruler vertically to the lowest part of the nest cup, placing a second ruler horizontally bridging the opposite edges of the scrape, and reading the depth at their intersection (figure 3.1). Nest cup diameter (cm) was measured with the horizontal ruler in two directions perpendicular to each other (as most cups were slightly oval). The shape of the nest cup (shallow and wide or deep and...
narrow) was expressed as the depth of the nest cup divided by the surface area (= cup depth/diameter 1 x diameter 2).

The nests were revisited after they were vacated by the birds (clutches hatched or predated). Nest cup depth was measured again and the nest lining was collected into a small plastic bag. The depth of the empty scrape (cm) was measured after removal of the nest lining. The thickness of nest lining (cm) was calculated by subtracting nest cup depth from scrape depth (figure 3.1).

The collected lining material was dried in open plastic beakers close to the heating radiators in the field station, until their mass did not decrease anymore. Per nest we measured total (dry) mass (g) of the nest lining, its total volume (cm³, based on height in the beaker after drying and gentle shaking), and the relative contribution to the total volume of different types of lining material (estimated visually in c. 10% classes): willow leaves (Salix polaris or S. reptans), Thamnolia vermicularis (a lichen forming loose white filamentous thalli), other lichens, sedge/grass leaves and stems, moss, and other materials. In four nests of little stint that predominantly consisted of willow leaves, we counted the number of leaves included.

**Approximating insulative properties of nests**

Newton’s law of cooling states that a heated object (in this case an egg) cools down to ambient temperature according to \( T_{egg} = T_i + (T_i - T_a) \exp(-C \times \text{time}) \) with \( T_i \) and \( T_a \) the initial and final temperatures of the egg respectively (°C) and the exponential cooling coefficient \( C \) (s⁻¹) depending on the thermal properties of the object and its environment. Based on this principle, Reid et al. (2002) measured the insulative properties of pectoral sandpiper nests by determining \( C \) from the cooling curve of pre-warmed clay eggs placed in them, and quantified the relative contribution of several nest features. They found that in deeper nests eggs lose more heat to the surrounding soil, but at the same time they are more sheltered from the cooling effect of wind. A thicker lining reduces heat loss, while the insulative performance varies between types of lining material and decreases when the material is wet.

We used the quantitative relationships derived empirically by Reid et al. (2002) to reconstruct the effect of these factors on the egg cooling coefficient for every nest of the six species in our study based on their dimensions and lining composition. We did this by estimating the proportional difference in \( C \) between a nest with the measured dimensions and a nest with average dimensions for pectoral sandpiper (nest cup depth 3.1 cm, diameter 9.1 cm, lining depth 2.1 cm, lining material 50% grass, 30% leaves, and 20% lichens). Our aim was not to derive a precise absolute prediction of the cooling rate of eggs in our nests, but to be able to compare and combine the relative effects of different nest features in a way that is consistent with heat loss theory.

Eggs in deeper nest cups are closer to the permafrost and therefore surrounded by colder soil, which increases heat loss to the ground. To estimate this effect of nest cup depth we used figure 2 of Reid et al. (2002). For nest cup depth ≤3.1 cm the egg cooling coefficient did not depend on cup depth; in the range 3.15 to 7 cm, \( C \) increased by 0.64 x10⁻¹ per cm depth. On the other hand, deeper nest cups are better protected from wind as illustrated by the fact that the gradient of the wind speed vs. cooling coefficient relationship declined significantly with increasing scrape depth. Reid et al. (2002) worked with nests of a single species and used cup depth as the predictive variable, but we compare nests of different species varying not only in depth but also in diameter. We assumed that the cooling effect
of wind is proportional to the ratio of the surface of the nest cup-air interface and nest cup depth. Therefore, we rescaled Reid et al. (2002)’s figure 3 predicting the gradient between surface wind speed and egg cooling coefficient using \((\text{cup depth/diameter}^2)\) as the predictor variable instead of cup depth. This yields the equation: gradient = \((0.29-0.29 \times \text{(cup depth/diameter}^2))\times10^3\).

Heat loss to the ground decreases nonlinearly with lining depth, with the strongest reduction when lining depth increases from 0 to 2 cm but little extra effect of a thicker layer (Reid et al. 2002, figure 4). The relationship between lining depth and egg cooling coefficient was described by: \(C = 3.1+7 \exp(-1.3 \text{ lining depth})\). Cooling coefficients also varied significantly between eggs surrounded by different materials and increased in the order: salix leaves, grass, \text{Thamnolia}, other lichens and moss. In wet conditions egg cooling coefficients increased for all materials. To account for the effect of different nest lining materials, we calculated an aggregated (weighted mean) nest lining material cooling coefficient based on the assumption that nest lining is dry for 2/3 and wet for 1/3 of the time.

An estimate of the combined effect of these three nest features on nest insulation was derived by multiplying the proportional differences in egg cooling coefficient between the measured nest and an average pectoral sandpiper nest for each of the effects described above, with the value of \(C\) predicted from these same equations for a typical pectoral sandpiper nest. Egg cooling rates were predicted for a wind speed of 5 m/s, a value typical for our study area during the incubation period (Schekkerman et al. 2004).

**Statistical analyses**

To analyse permafrost depth in relation to date we took into account that multiple observations per nest were carried out and used Linear Mixed Models (the REML directive in Genstat 8). Nest was entered as a random term and day + day\(^2\) and species were entered as fixed effects. To test for differences in slopes between species, we also included interactions.

Nest measurements such as scrape depth, nest cup depth, nest lining depth were averaged per species and plotted against mean body mass for the different species. As we did not measure individual body mass for the owners of the individual nests, we used the mean

**Figure 3.2.** Distribution of breeding sites of six shorebird species with number of nests in brackets. The upper bar represents the relative occurrence of the different categories in the study area.
body mass per species (measured during incubation, Schekkerman et al. 2004). Instead of using untransformed body mass, we applied an exponent of 0.73, to account for metabolic activity of the differently sized species (Aschoff and Pohl 1970). The relationship between nest measurements and body mass$^{0.73}$ was investigated using linear regressions, weighed for the inverse of the standard error in the specific nest measurement, to account for the variation.

**Results**

**Breeding site**

The majority of shorebird nests that were located on a slope were oriented towards the south, but sometimes also to the west, east or north side (figure 3.2). In curlew sandpiper and red phalarope a relatively large proportion of nests was found in flat lowland. Most dunlin nests were found on flat ridge tops. However, there was no difference in mean rank score of thermal favourability between species (Kruskall-Wallis nonparametric ANOVA, $H_6 = 4.08$, $P = 0.54$), and mean rank scores were not related to body mass$^{0.73}$ ($F_{1,4} = 0.16$, $P = 0.70$). The mean rank score for thermal favourability for all shorebird nests combined (2.54) differed significantly from the average of the study area (3.20, $\chi^2 = 51$, df = 4, $P < 0.001$).

**Depth of permafrost**

The depth of permafrost was 5 cm at the start of breeding in late June and increased to > 50 cm in late July (figure 3.3). The permafrost depth decreased significantly nonlinearly with the progressing season with a different intercept for the different species, but the rate of change did not differ between species (day: Wald = 1785, $P < 0.001$; day$^2$: Wald = 34, $P < 0.001$; species: Wald = 15, $P = 0.006$; day.species: NS; day$^2$.species: NS, figure 3.3). The intercept decreased in the order: Pacific golden plover, ruddy turnstone, dunlin, red phalarope, curlew sandpiper, little stint. However, the depth of permafrost at egg laying did not correlate with body mass$^{0.73}$ ($F_{1,4} = 0.58$, $P = 0.487$).

![Figure 3.3. Depth of permafrost in relation to date in six species. The regression lines for the two extremes are given.](image-url)
Nest cup depth and scrape depth

Nest cup depth varied between 1.5 and 7.0 cm, while scrape depth (depth of nest cup without the lining material) varied between 3.1 and 10.0 cm. The largest variation between nests was found in red phalarope. Nest cup depth was not correlated with body mass$^{0.73}$ ($F_{1,4} = 0.11$, $P = 0.758$). Scrape depth, however, decreased with body mass$^{0.73}$ ($F_{1,4} = 5.56$, $P = 0.078$, $R^2 = 47.4$, Figure 3.4 left). The shape of the nest differed significantly between species ($F_{1,4} = 35.42$, $P = 0.0.004$, $R^2 = 87.3$) with relatively narrow deep nests in little stints and wide, shallow nests in Pacific golden plover and turnstone. The measure for nest shape, nest cup depth/diameter$^1$ *diameter$^2$ significantly increased with body mass$^{0.73}$ ($F_{1,4} = 7.02$, $P = 0.057$, $R^2 = 54.6$, Figure 3.4 right).

Figure 3.4. Nest cup and scrape depth (left) and nest cup depth/diameter$^2$ (right) in relation to body mass$^{0.73}$. LS = little stint, PH = red phalarope, DU = dunlin, CS = curlew sandpiper, TU = turnstone, PGP = Pacific golden plover. Average and SE values are represented for each species.

Nest lining depth and dry mass

Eggs in the freezer
Figure 3.6. Nest lining material used by six different shorebirds with number of nests in brackets.

Figure 3.7. The relative contribution of cup depth to heat loss to the ground (upper left), of cup depth on wind cooling at 5 m/s (lower left), of lining depth (upper right) and of lining material (lower right) to egg cooling rates in relation to body mass. LS = little stint, PH = red phalarope, DU = dunlin, CS = curlew sandpiper, TU = turnstone, PGP = Pacific golden plover. Average and SE values are represented for each species.
Lining thickness and material

The thickness of nest lining varied between 0.1 cm and 7.6 cm, was thickest in the smallest species and decreased significantly with body mass \(^{0.73}\) \((F_{1,4} = 35.4, P = 0.004, R^2 = 87.3,\) figure 3.5 left). Also dry mass of the nest lining showed a significant decrease with body mass \(^{0.73}\) \((F_{1,4} = 22.2, P = 0.009, R^2 = 80.9,\) figure 3.5 right). Little stint nearly exclusively used leaves of the two willow species present, \(S.\) reptans and \(S.\) polaris (figure 3.6). This was also important nest material for dunlin, curlew sandpiper and red phalarope. Red phalarope was the only species that lined the nest with a large proportion of grass and sedges. Ruddy turnstone and Pacific golden plover preferred to line their nests with the lichen Thamnolia vermicularis supplemented with other lichens, willow leaves and a small fraction moss. Moss was used by all species in very small quantities, except red phalarope.

The number of willow leaves in four nests of little stints were 919 (90\% \(S.\) reptans, 10\% rest grass/moss), 1372 (80\% \(S.\) polaris, 15 \(S.\) reptans, 5\% rest grass/moss) 1810 (90\% \(S.\) polaris, 10\% rest grass/moss) and 1918 (50\% \(S.\) polaris, 50\% \(S.\) reptans), respectively. The willow leaves were not freshly picked by the birds but were old dry ones from previous years, a resource that can be very abundant locally.

Composite approximation of egg cooling coefficient

The effect of nest cup depth on the proportion difference in cooling coefficient through heat loss to the ground was not correlated with body mass \(^{0.73}\) \((F_{1,4} = 0.95, P = 0.386,\) figure 3.7 upper left). The sheltering effect of the nest cup at wind speed of 5 m\(\text{s}^{-1}\) on the cooling coefficient significantly increased with body mass \(^{0.73}\) \((F_{1,4} = 35.42, P = 0.004, R^2 = 87.3,\) figure 3.7 lower left).

The effect of nest lining depth on egg cooling showed a significant increase with body mass \(^{0.73}\) \((F_{1,4} = 7.37, P = 0.053, R^2 = 56.0,\) figure 3.7 lower left). The effect of nest material on the egg cooling coefficient increased significantly with body mass \(^{0.73}\) \((F_{1,4} = 21.12, P = 0.010, R^2 = 80.1,\) figure 3.7 lower left).

The four separate effects described above were aggregated into one effect on egg cooling at a wind speed of 5 m\(\text{s}^{-1}\), a value normal for this area in summer (Schekkerman et al. 2004, figure 3.8). This cooling coefficient increased significantly with body mass \(^{0.73}\) \((F_{1,4} = 19.33, P = 0.012, R^2 = 78.6).\) Thus the contribution of the different adaptations to reduce heat loss is relatively larger in the smaller species.

**Figure 3.8.** The predicted egg cooling coefficient in wind of 5 m/s in relation to body mass \(^{0.73}\).

LS = little stint, PH = red phalarope, DU = dunlin, CS = curlew sandpiper, TU = turnstone, PGP = Pacific golden plover. Average and SE values are represented for each species.
Discussion

Nest design

We measured characteristics of shorebird nests and found significant relations of nest scrape depth, nest shape, thickness and type of lining material with species body mass. These patterns result in a stronger reduction of heat loss from nests of small species compared to nests of larger species. The distance between the surface and the permafrost declined with date and was largest in the larger species. All species seemed to have a preference for southerly slopes and selected the thermally favourable sites. This may be the result of the fact that south facing slopes are cleared of snow earlier in the season and available for nest building. The smaller species had deeper and narrower nests than the larger species, a pattern which has been described before (Ar and Sidis 2002). Our estimates of the egg cooling coefficients showed that eggs in nests of the larger species cool down more rapidly and the different adaptations to reduce heat loss have a stronger effect in the smaller species. A difference in nest size and insulation related to body size was also observed in two species of arctic breeding geese (McCracken et al. 1997).

Egg cooling coefficient calculations

Our estimates of egg cooling rates are based on extrapolation from the relationships derived in pectoral sandpiper nests using artificial eggs (Reid et al. 2002). The thermal properties and measured heat loss rates of the artificial eggs that were used in Reid et al. (2002) probably deviate from the values in real pectoral sandpiper clutches. In our interspecies comparisons there was no correction for egg size, but egg cooling rates referred to the situation where eggs of the size of those of pectoral sandpipers would have been put in the nests of the different species. Hence, also the interspecific differences in egg size will deviate from real measurements. Given the comparisons of relative values used in this study, we are confident that any pattern shown up using extrapolated relationships, would also appear if real eggs had been used. However, small eggs cool down more rapidly than large eggs (Ar and Sidis 2002), therefore the relations found will probably decrease in strength if the size effect is taken into account.

The nest with and without the incubating bird

We calculated egg cooling rates for the situation when the bird is off the nest. Most of the time (81-87%) even uniparental incubators are on their nest (chapter 4). In general, the smaller uniparental species leave the nest more often for shorter intervals than larger species, but total recess time does not differ between the species. But what happens when the bird is on the nest? If the parent returns to the nest the eggs need to be rewarmed. At the instant when the egg temperature reaches the steady state, the energy flow into the egg is the same as the energy flow going out of the egg. As Drent (1975) pointed out, at this moment the eggs are basically an extension of the bird’s body. The benefits of nest construction as shown for the situation without the parent present, are thus likely also valid in the situation with the incubating bird (Lamprecht and Schmolz 2004). Both lining material and lining thickness still contribute to the insulative properties (de Heij 2006). However the effect of wind cooling, acting through nest cup depth for the eggs in an open nest, will affect the incubating bird differently. But still the incubating bird will be better sheltered from the wind in deeper nest scrapes (Buttemer et al. 1987). This would mean that birds do not only stay on the nest because it is beneficial for the development of eggs, but also to conserve energy, as time spend away from the nest generally costs more energy than incubating the eggs (Piersma et al. 2003; Cresswell et al. 2004).
**Lining material**

That nest insulation is apparently important for especially the smaller species, suggests that the supply of lining material may determine nest site choice and habitat suitability. The choice of nest lining material naturally depends on what material is available. Of the two *Salix* species that were used as lining, *Salix polaris* predominated, but was also the most common in the area. From the selection found in shorebird nests, willow leaves had the best insulative properties. In the smaller species this was also the material that was used most. The material that retains warmth even better, down or feathers (Toien 1993; Lombardo et al. 1995; Reid et al. 2002; Lamprecht and Schmolz 2004; McGowan et al. 2004; Pinowski et al. 2006), was never used in any of the shorebird nests. The reason for this is probably not the lack of availability (feathers can be taken from own plumage), but the fact that cooling coefficient of feathers is strongly increased in wet conditions. When wet, the insulative effect of feathers has been shown to be degraded from the best to the second worst in the row: feathers, *Salix* leaves, grass, lichen and moss (Reid et al. 2002; Hilton et al. 2004). Considering that weather in the tundra is often humid and foggy, feathers are probably not as suitable here as in other areas (or in closed nests). Another reason to avoid using feathers is that they may attract predators through their smell (Reneerkens 2007).

The effect of lining depth was relatively important compared to other effects (figure 2.7). The thickness of nest lining showed considerable variation within individual nests of the same species (figure 2.5). Although we do not have the proper measurements to test this hypothesis, this individual variation might well be explained by differences in microclimates to which birds adapt the amount of lining. In an experiment where the amount of nest material was manipulated, the parents restored original amount of nest material both in nests where nest material was reduced and increased (Szentirmai and Szekely 2002). Parents apparently carefully balance the various costs and benefits of nest material use during incubation. Further evidence that birds adjust the amount of nest lining to environmental conditions is provided by McGowan et al. (2004), who describe that long-tailed tits *Aegithalos caudatus*, whose nests were provisioned with extra feathers, compensated for this by reducing the number of feathers they brought in themselves.

**Why don’t large waders insulate their nest better?**

Our analysis showed that the smallest species of shorebirds invested most in nest insulation. The smallest species in our sample also all happen to be uniparental species: little stint, red phalarope and curlew sandpiper, while the two larger species (Pacific golden plover, turnstone) are biparental. Dunlin is the only small species in our sample with a biparental care system.

This makes it impossible to disentangle effects of the parental care system and body size on nest construction. The reason why the small uniparental species that face the highest energetic demands (Piersma et al. 2003) try to optimise nest insulation seems obvious. Also from other studies it has been shown that nest insulation can have an important effect on incubation effort and hatching success (Grubbauer and Hoi 1996). So why do the larger biparental species not adopt this energy saving strategy and insulate their nests better?

First of all, the costs of a poor insulation may not be so high for larger species. Apart from an energetically more beneficial surface to volume ratio, they also produce bigger eggs, that cool down slower than smaller eggs (Turner 2002). Furthermore the larger species in our sample are all biparental, which means the eggs are rarely left alone and incubation is near constant (Norton 1972; Cresswell et al. 2003). This prevents the eggs from cooling...
down during foraging trips. Especially rewarming eggs upon return from a recess period elevates energy expenditure for the incubating parent (Vleck 1981; Biebach 1986).

Secondly the benefit of a better nest insulation might not outweigh the costs associated with the extra effort. A deeper scrape needs more work excavating and the nest material has to be collected. From accidental observations in the field we know that most of the nest material is brought to the nest item by item. This can take considerable time and effort. Especially to collect large amounts of small willow leaves, the material with the best insulative properties, will require a lot of time (e.g. little stint nests contained 1000-2000 leaves).

The larger species tended to nest in different habitat than the smaller species. Pacific golden plover and turnstone generally nested in drier tundra often characterised as frost-boiled tundra where lichens, bare soil, grass and herbs predominate (cf Chernov 1985). Little stint, curlew sandpiper and dunlin nest in wetter habitat with more dry willows leaves present. Not all materials are equally abundant everywhere. Of course this is a circular argument; the larger species could choose to nest in areas where the most profitable nest lining material can be obtained, but there are apparently other (more important) reasons why they nest where they do.

Arctic breeding shorebirds rely heavily on their extremely well-camouflaged eggs, and in most cases also plumage, that makes it very difficult for predators to find the nests. The use of local materials can improve the strong crypsis and this benefit may outweigh the benefits of a better insulating lining. The extreme of this trade-off between thermal properties and camouflage has resulted in a nest consisting of pebbles only, such as found in the ringed plover, a species co-occurring in the same area in low numbers. The lichen Thamnolia often used by Pacific golden plover and turnstone provides a much better camouflage in the habitat where these species breed than some of the better insulating materials.

Finally biparental species tend to start breeding earlier than uniparental species (Whitfield and Tomkovich 1996; Schekkerman et al. 2004). At the onset of spring the permafrost is still relatively close to the surface and making a deep scrape might simply be impossible, or the cooling caused by the proximity of the ice outweighs the advantage of a deep scrape. By the time that uniparental species start nesting, the permafrost has retreated deep enough to be limiting the scrape depth.

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The arctic pulse

Op het moment dat de eieren worden gelegd, half juni, zit de vorst nog stevig in de grond. De permafrost ontdooit, zoals de naam al zegt, nooit helemaal, maar de diepte waarop deze diepgerezen laag begint zakt in de loop van de zomer tot bijna een halve meter onder het toendraoppervlak. Op het moment dat de meeste soorten steltlopers beginnen met broeden ligt de bovenkant van de permafrost zo’n 10 cm onder het oppervlak. Als je bedenkt dat de nestkuil ongeveer 3-10 cm diep is, liggen de eieren dus zo goed als op het ijs.

en verliezen daardoor relatief minder snel warmte. Voor de kleinere soorten waarvan het nest bebroed wordt door slechts één van de ouders en die hun nest regelmatig noodgedwongen alleen laten om voedsel te zoeken, is een goede isolatie daarom waarschijnlijk belangrijker. Dat maakt het moeilijk om onderscheid te maken wat het verschil in nestbouw veroorzaakt: het feit dat ze alleen broeden of de grootte van de soort. Het meest waarschijnlijk is dat het er allebei toe doet.

Naast het feit dat het natuurlijk meer werk is om al dat nestmateriaal te verzamelen, kan het ook zo zijn dat de camouflage van het nest belangrijker is dan een goede isolatie. Op de drogere plekken waar de grotere soorten broeden komen meer korstmossen en minder wilgen voor. Een nest bekleed met lokale materialen, in dit geval korstmossen zal daar waarschijnlijk minder opvallen. Aan de andere kant zou het natuurlijk ook zo kunnen zijn dat kleine strandlopers misschien alleen op die plekken kunnen broeden waar voldoende wilgenblaadjes voorhanden zijn.