The arctic pulse
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Chapter 4
Time allocation between feeding and incubation in uniparental arctic breeding shorebirds: energy reserves provide leeway in a tight schedule

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Birds with uniparental incubation may face a time allocation problem between incubation and feeding. Eggs need regular warming to hatch successfully, but the parent must leave the nest to feed and safeguard its own survival. Time allocation during incubation is likely to depend on factors influencing egg cooling rates, parental energy requirements and feeding intake rate. How this allocation problem is resolved was subject of this study on arctic breeding shorebirds. We compared incubation rhythms between four uniparental shorebird species differing in size and expected to find both species differences and weather effects on the organisation of incubation.

Attentive behaviour and responses to variation in weather showed a remarkable consistency across species. All species alternated feeding bouts (recesses) with brooding bouts throughout the day. Recesses were concentrated in the warmer parts of the day, while recess duration showed little diurnal variation. Despite continuous daylight, a pronounced day-night rhythmicity was apparent. The four species in this study spent a similar proportion (13-19%) of the time off their nest. After correction for weather effects, the number of recesses was largest in the smallest species, while recess duration was longest in the largest species. Total recess time per day increased on cold days through an increase of mean recess length, while the number of recesses decreased. Comparing our observations to predictions derived from criteria that birds might use to organise their attentive behaviour, showed that the limits are set by parental requirements, while the energy stores of adults provide some leeway for short-term adjustments to environmental variability.

If breeding birds trade off feeding time against incubation time, energy stores are expected to be influenced by weather. We expected uniparental species to be more likely to show weather effects on condition than biparentals, as in the latter ‘off duty’ time is much larger and independent of weather. This prediction was tested by comparing energy stores in two uniparental species and a biparental congener. While body mass of uniparental incubators decreased after a period with low temperatures, body mass of the biparental species did not.
Introduction

Many systems of parental care coexist in shorebirds (Charadrii). Apart from the biparental system in which both parents share incubation and chick-rearing duties, a variety of systems occur with unbalanced parental duties (Reynolds and Szekely 1997). At the extreme of these, one bird carries out all incubation duties (‘uniparental incubators’). Due to their small size and high mass-specific metabolic rates, shorebirds have a limited capacity to store energy before the onset of breeding and therefore they have to feed during incubation.

When eggs are not incubated, embryo development is assumed to continue as long as egg temperature exceeds c. 26°C (Drent 1975; Webb 1987; Ewert 1992). Long periods of absence, during which egg temperature drops below this value, result in a slowing or ceasing of embryonic development, and prolong the total incubation period (Webb 1987), with possible adverse effects on hatchability and offspring condition, and an increase in exposure time to predation. Reproductive output can thus be reduced because the parent spends too much time away from the nest, but a reduction of feeding time may put the parent’s own survival and hence both current and future reproduction at risk. The way this allocation problem is resolved is likely to depend on factors influencing both egg cooling rates and parental energy requirements and feeding intake rate.

Incubation has long been considered energetically inexpensive, but recent studies have shown that this is not true (Williams 1996), especially not in arctic environments (Tinbergen and Williams 2002; Piersma et al. 2003; Cresswell et al. 2004). This further complicates the time allocation problem of uniparental incubators: in cold conditions eggs cool faster, while energy expenditure for thermoregulation increases. Also, during cold, windy or rainy spells which are a regular feature of arctic weather even in summer, the availability of arthropods, an important food source for many tundra-breeding shorebirds, is drastically reduced (as measured by pitfall traps, Schekkerman et al. 2003) and food intake by the parent may easily fall short of energy demands.

To investigate how parents resolve this allocation problem, we collected data on incubation rhythms in four uniparental arctic breeding sandpiper species co-occurring in the same area in Taimyr, Siberia, but differing in size (30-67 g): little stint *Calidris minuta*, red phalarope *Phalaropus fulicarius*, pectoral sandpiper *Calidris melanotos* and curlew sandpiper *Calidris ferruginea*. If energetic considerations limit incubation performance, we expected that (1) incubation behaviour changes when conditions determining energy expenditure or uptake (e.g. weather) change, (2) incubation behaviour in small species is more time-stressed than in large species (3) severe conditions cannot be fully buffered by behaviour and lead to a reduction in offspring viability or a decrease in parental condition. If the energetic constraint is a direct consequence of the uniparental nature of incubation, these effects should not be apparent in biparental incubators.

Since large eggs cool slower than small ones, and mass-specific field metabolic rate (FMR) during incubation is lower in large than in small birds (Tinbergen and Williams 2002, Piersma et al. 2003), the optimal behavioural response to weather variations may differ for differently sized birds. Therefore we expect any weather effects on incubation behaviour to be less pronounced in larger species.

If birds trade off feeding time against incubation time to increase the viability of their eggs, energy stores, reflected in body mass, are expected to be influenced by periods of adverse weather. We expect that uniparental incubators are more likely to show such condition effects than biparental species, as in the latter ‘off duty’ time is generally much larger, and does not vary with weather conditions. In this paper we compare weather
effects on body mass of two uniparental species, little stint and curlew sandpiper with those in dunlin *Calidris alpina*, a similar-sized congeneric biparental species, co-occurring in the same area.

**Methods**

*Study area and species*

We studied the incubation behaviour of shorebirds at Medusa Bay, 18 km south of Dikson on the Taimyr peninsula, Siberia (73°20’N 80°30’E) between June and August in 2000 and 2001. The habitat consists of hilly arctic tundra (*cf.* Chernov 1985) with a rolling relief between 0 and 50 m above sea level, and scattered stony ridges. Vegetation consisted of moss, lichen, grass and sedges, generally not higher than 10 cm with a significant proportion of the surface bare. During the complete study period the sun never set. However light intensity varied throughout the day, resulting in lower temperatures in the night and differences between daily minimum and maximum temperature ranging from 0.5 to 14.5°C.

We studied four small shorebird species with uniparental care, but differing in mating system. In the polyandrous red phalarope (RP) the female’s contribution to reproduction is limited to egg laying and all incubation is done by the male (Cramp and Simmons 1983). In curlew sandpipers (CS) and pectoral sandpipers (PS) females incubate the eggs and raise the chicks, while males desert after clutch completion (Cramp and Simmons 1983; Tomkovich 1988). Little stint (LS) females produce two clutches of which the first is usually incubated by the male and the second by the female, always without help from a partner (Hildén 1978). The four species differ in body mass and egg mass (table 4.1). The fraction of body mass that the clutches represent amounts to 70% (RP), 74% (CS), and 82% (LS and PS). All four species lay a typical shorebird clutch of four eggs.

*Weather data*

In 2000, data on precipitation (mm/day) and wind (m/s) were provided by the meteorological station in Dikson, 18 km north of the study area. Air temperature (using a thermistor placed at 1 m height in the shade) was measured every half hour on location and stored by data-loggers. In 2001 all weather data were recorded every half hour at our study site using an automated weather station. Air temperature was recorded at 1 m height in the shade, wind speed at 10 m.

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**Table 4.1.** Mean body mass and (fresh) clutch mass of the four uniparental species. Egg data for LS, RP, PS: Cramp and Simmons 1983, CS: Tomkovich, pers. comm. Body mass data: Schekkerman et al. 2004.

<table>
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<tr>
<th>species</th>
<th>body mass (g)</th>
<th>SD</th>
<th>N</th>
<th>clutch mass (g)</th>
<th>ratio</th>
</tr>
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<tr>
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<td>29.2</td>
<td>2.6</td>
<td>213</td>
<td>24</td>
<td>0.82</td>
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<tr>
<td>red phalarope (RP)</td>
<td>51.1</td>
<td>6.8</td>
<td>6</td>
<td>36</td>
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<tr>
<td>pectoral sandpiper (PS)</td>
<td>63.3</td>
<td>4.6</td>
<td>9</td>
<td>52</td>
<td>0.82</td>
</tr>
<tr>
<td>curlew sandpiper (CS)</td>
<td>64.7</td>
<td>4.2</td>
<td>28</td>
<td>48</td>
<td>0.74</td>
</tr>
</tbody>
</table>
Incubation

Nests were located by intensive searching during and after the laying period. The developmental stage of eggs was determined by flotation (Van Paassen et al. 1984; Schekkerman et al. 2004). Nests were marked and checked approximately every three days. When a clutch failed prematurely, the cause was determined. If eggs were cold and wet it was considered deserted, if eggs were gone and no small shell fragments (indicating that eggs had hatched) were found in the nest, we assumed it was depredated.

Incubation schedules were recorded from nest temperature measurements carried out with small waterproof data loggers (Tiny Tag, Gemini), programmed with GLM (Gemini Logger Manager) software. A temperature-sensitive probe (2 x 5 mm, temperature range -10°C to 50°C) was connected to the loggers with a thin electrical wire. The probe was attached to the ground with a pin and positioned just below the apices of the four eggs in the centre of the nest cup, so that it touched the brood patch of the incubating bird. Storage capacity of the loggers allowed >11 days of temperature recording at 1 minute intervals. The loggers were covered with moss to avoid attracting predators. The loggers were collected after chicks had hatched or the nest was depredated, or replaced after 11 days. Start and end of incubation recesses were determined from graphs of temperature against time. Because ambient temperature was always much lower than nest air temperature during incubation (figure 4.1), no problems were encountered with the interpretation of the graphs. Recesses shorter than one minute were not recorded, but from visual observations we know that these occur rarely. In most cases the probe stayed well in place, but sometimes movements of the bird caused a displacement resulting in irregular temperature graphs. Such recordings were discarded. Recordings around hatching were excluded because incubation behaviour became irregular after eggs were pipped, and difficult to interpret once chicks were in the nest.
Nest attendance was described using three parameters: total recess time (in % of 24 hour period), number of recesses per hour or per 24 hours, and mean recess duration. Visual time budget observations on LS and CS confirm that birds spend > 90% of the recess time foraging (T. Kirikova unpubl. data). Mostly during the ‘night’, and sometimes during cold days, birds tended to stay on the nest continuously. Such a ‘period of continuous incubation’ was considered to start/stop when birds stopped/started leaving the nest at regular intervals (< 1 h). Start and end times could be determined for a total of 217 periods of continuous incubation in LS (47 nests), 77 in CS (15 nests) and 72 in PS (8 nests). Sample size of these periods in RP was too small to allow analysis.

The complete dataset, incorporating both complete 24 hour periods and measurements that did not span complete 24 hour periods, was used to describe diurnal variation in incubation behaviour. In total data of 61 LS, 15 CS, 8 PS and 2 RP nests were used including respectively 7647, 2139, 2005 and 370 recesses (and as many incubation bouts). To analyse the effect of time of day and differences between species, Linear Mixed Models (REML directive in Genstat, Genstat 1993) were used, taking into account different levels of variation in the observations (between and within nests). For this analysis number and duration of recesses and total recess time were averaged per hour per nest. Nest number was entered as a random effect and hour\textsuperscript{1}, hour\textsuperscript{2} and hour\textsuperscript{3} as fixed effects. Thereafter we investigated whether any of these patterns differed significantly between species by entering species as the final term.

A subset of the measurements, including only those that comprised complete 24 hour periods, were used to analyse effects of weather and day relative to hatching on attentive behaviour. In total 197, 91, 64 and 13 such periods were available, collected in nests of 38 LS, 15 CS, 7 PS and 2 RP respectively.

Proportion recess time was arcsin-transformed, and natural logarithms were taken of the number of recesses per 24 hours to improve the validity of normality assumptions in the analyses. Weather and other effects were analysed using Linear Mixed Models with nest as random effect and 24 h means of air temperature, wind speed, amount of precipitation, and day relative to hatching as fixed effects. For analysis of lengths of periods of continuous incubation, weather variables were averaged over the period between 20.00 and 08.00 hours; the period of uninterrupted incubation always fell within this time window.

During some measurements exceptionally long recesses took place. Analyses were performed both including (‘full data’) and excluding 24 hour measurements with long absences (‘reduced data’). The full dataset shows under what conditions long absences occur, but because of their extreme length they mask small-scale patterns that exist in the regular rhythm. Because we did not \textit{a priori} know whether long absences are induced by disturbance or weather-related, we analysed the probability of periods of long absences in relation to weather in the full dataset using a logistic regression with nest, air temperature and wind speed as predictor variables.

\textbf{Body mass}
Most LS, CS and biparental dunlins (DU) were caught on the nest using a small clapnet and weighed to the nearest 0.1 g in the second or third week of incubation. Since this was done only once and usually not simultaneously with recordings of incubation rhythm, body mass was not included in the analyses of incubation behaviour. However, we investigated the effect of weather prior to weighing on body mass, to see if feeding time limitation due to incubation affected condition in cold periods. After a correction for size (wing length,
the best predictor for body mass in the three species) a series of weather variables was tested in a procedure that compares all possible models to identify the best explaining weather variables for each species (based on AIC). Effects of air temperature, wind speed and total precipitation averaged over the day of weighing, over the day before weighing, over the last three days (including the weighing day) and over the last five days were tested. The effect of incubation stage (day relative to hatching) was also tested. Weights obtained on the day prior to or on the hatching date were excluded, because a sudden drop in body mass linked to hatching of the chicks commences around that day (Soloviev and Tomkovich 1997: chapter 5). Too few PS and RP were caught for this analysis. Dunlins were sexed based on bill length and plumage; CS were all females (males do not incubate); LS were not sexed because this can not be done reliably based on morphometrics.

**Results**

*Patterns in incubation rhythm within days*

An example of a nest attendance recording is presented in figure 4.1. In all four species, short (1-20 minute) bouts of absence and presence on the nest were alternated from early mornings until late evenings. During the coldest part of the day, mostly between 2000 and 0800 hours, birds generally incubated continuously and left the nest only for a few short periods. Deviations from this pattern were sometimes found during adverse weather, such as storms, heavy rain or snowfall, and also in exceptionally warm conditions.

Before investigating variation between days, we first analysed how incubation rhythms vary throughout the day and how species differ in this respect (reduced dataset only). Mean number of recesses per hour was highest in the warmest part of the day and lowest during the ‘night’ for all four species (figure 4.2). After correction for diurnal patterns (effects of hour1, hour2 and hour3 all P < 0.001, Wald tests of Linear Mixed Models), the mean number of recesses differed significantly between species (Wald test: $\chi^2 = 23$, P < 0.001) and decreased in the order LS > PS > RP > CS (figure 4.2). Only the pairwise differences between CS and LS and CS and PS were significant. Mean recess length differed between species and increased in the order LS < RP < PS < CS (figure 4.2). The pairwise difference between LS and CS was significant. No interspecific differences were found in mean total recess time per hour (Wald test, $\chi^2 = 1$, P = 0.85)

*Factors influencing incubation rhythms: 24 hour measurements*

A special feature of a minor proportion of the incubation measurements was the occurrence of long absences (1-8 hours). For a justified treatment of the data, it is important to know if these long absences represented a functional aspect of incubation behaviour, or should be regarded as ‘noise’ created by factors such as prolonged disturbances by potential predators.

Long absences occurred in recordings at several nests (11 LS, 4 CS, 3 PS) in all species except red phalaropes. The probability of long absences in LS decreased with air temperature and increased with wind speed (figure 4.3, logistic regressions with nest as factor, LS: temp: P = 0.005, wind speed: P < 0.001). In CS and PS the probability of long absences was only related to air temperature (for both species P < 0.001). Given their occurrence during adverse weather conditions, we conclude that long absences were an integral part of the incubation decisions of the birds, and the data are presented accordingly. First we describe results for the full dataset, and then report how results change if long absences are excluded. Average values for incubation parameters are given for both datasets in table 4.2.
Figure 4.2. Mean number (± SD) of recesses (top), mean recess length (middle) and total recess time (lower) in the four species in relation to time of day.
Thereafter, statistical analyses to evaluate weather effects on incubation behaviour within species are only performed on the reduced set (because here we are mainly interested in the organisation of incubation schedule on a small time scale). The interspecific analysis was carried out on both sets.

Total recess time varied between species from 3.1 h in RP to 4.5 h in LS (13-19% of the day, table 4.2, figure 4.3). The number of recesses per day varied from 21.6 times in CS to 33.5 times in LS, and mean recess length varied from 7.2 minutes in RP to 15.3 minutes in CS. When excluding long absences, total recess time and mean recess length are shorter, but the difference is relatively small, due to the scarcity of these long absences (table 4.2).

In all species air temperature and/or wind speed explained a significant proportion of the variation in all three parameters (table 4.3), with longer total recess time and longer, but fewer recesses in colder conditions. The only exception is total recess time in CS, for which no significant effect of any of the variables was found. Furthermore, number of recesses per day increased during days with precipitation. In CS and PS also recess length
Figure 4.3. Absence of nest (% of 24 h period, bottom panel), recess length (minutes, middle panel) and number of recesses per day (top panel) in relation to air temperature in the four species (closed symbols = excluding the long absences, open symbols = including long absences).
was influenced by precipitation, resulting in more but shorter recesses in rainy weather (table 4.3). Day relative to hatching explained a significant proportion of the variation in total recess time only in PS; recess time increased in the later stages of incubation. In RP no significant effects of any of the variables tested were found.

**Interspecific patterns in incubation schedules**

Total recess time did not differ between the four species after correction for weather effects (table 4.4). For the number of recesses per day, ‘species’ contributed significantly to the model after correction for air temperature, wind speed and precipitation, with most recesses found in the smallest species (LS) and fewest in the largest of the four (CS). Species pairs that differed significantly were: CS - LS, CS - PS and LS - RP.

If the data are analysed excluding long recesses, results hardly differ. For recess length also a significant species effect was found: it decreased in the order CS > RP > PS > LS, but only the difference between CS and LS was significant.
Figure 4.4. Start and end of continuous incubation period in relation to air temperature. Lines are linear regressions.
Period of continuous incubation
During most ‘nights’ birds stayed on the nest continuously for a prolonged period. Mostly a few short recesses took place (figure 4.1). In all three species analysed (LS, CS and PS) the length of the period of continuous incubation increased with decreasing air temperature and/or increasing wind speed (figure 4.4; CS: temp: $\chi^2 = 7.22, P = 0.008$, wind speed $\chi^2 = 7.07, P = 0.008$; PS: temp NS, wind speed: $\chi^2 = 8.41, P = 0.004$; LS: temp: $\chi^2 = 27.94, P < 0.001$, wind speed $\chi^2 = 8.23, P = 0.004$). The end of the period of continuous incubation was more strongly affected by weather than its start (figure 4.4). In none of the species did day relative to hatching explain a significant proportion of the variation.

Hatching success
Incubation inconstancy could lead to retarded egg development or nest desertions. Therefore we analysed the frequencies of these events in the four uniparental breeders and in the biparental dunlin.

In both years predation rates were very high, with hatching probabilities for LS: 0.01 and 0.18, CS: 0.00 and 0.09, in 2000 and 2001 respectively (calculated using Mayfield 1970, Tulp and Schekkerman 2001). PS and RP only bred in the area in 2001 with hatching probabilities of 0.32 and 0.58 respectively. Hatching probabilities for dunlin were 0.03 and 0.24 for

Table 4.4. Results of REML analyses of interspecific patterns in incubation rhythms for full and reduced dataset separately. See table 4.2 for definition full and reduced dataset.

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<th>df</th>
<th>P</th>
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4 Nest attentiveness in uniparental shorebirds
Figure 4.5. Residual (standardized) body mass of little stints and curlew sandpipers (after correction for wing length) in relation to the best explaining weather-related variable (mean temperature on the last three days before catching).

Figure 4.6. Residual (standardized) body mass (after correction for wing length) in male and female dunlin in relation to the best explaining weather-related variable (mean temperature on the day before catching).
the two years. In most surviving nests, all four eggs hatched successfully. Partial hatching caused by no or retarded development was not observed in 2000 and occurred in four LS nests, one RP, one PS and one DU in 2001.

In CS none of the 29 nests under observation in 2000 and 2001 was deserted. Nest desertions occurred in 17 of 200 LS nests, in one of four RP nest and in one of 12 PS nests. In dunlin one out of 54 nests was deserted. Most of these desertions were likely to be the result of disturbance by observers, or caused by a herd of >1000 reindeer Rangifer tarandus passing through the area and grazing in the proximity of nests on one day in 2001. Five were deserted because of other reasons and were among the latest hatching nests of the season (late July). Two of the ‘naturally deserted’ nests contained newly hatched young or partially hatched eggs at the time of desertion.

Body mass
To investigate the effect of weather on body mass, birds should ideally be recaptured several times. However catching a shorebird on the nest is relatively easy, but recapturing is difficult and in PS and CS impossible, because birds once caught are more wary. Single body mass measurements of 170 LS, 51 CS and 53 DU were used to investigate correlations with weather on preceding days. After a correction for size (CS: \(F_{1,48} = 5.72, P = 0.021\), LS: \(F_{1,167} = 17.08, P < 0.001\)) the remaining variation was significantly reduced by weather-related variables in both uniparental species: body mass was higher after warmer weather (figure 4.5). Mean air temperature on the three days prior to weighing explained most of the variance in CS (including the catching day \(F_{4,48} = 6.26, P = 0.016, R^2 = 0.17\)) and in LS (\(F_{1,167} = 14.91, P < 0.001, R^2 = 0.15\)). In contrast, body mass of biparental dunlins, after a correction for size (\(F_{1,51} = 24.66, P < 0.001\)) did not show a relationship with any of the weather variables (figure 4.6). Day relative to hatching had no significant effect on mass in any species.

Discussion
Does a time allocation problem exist?
Bird embryos probably develop optimally when incubated continuously. Even if embryos of birds breeding in cold environments are relatively resistant to cold exposure (Webb 1987), egg neglect will lead to a lengthening of the incubation period, prolonging exposure to predators. Also, the time window favourable for raising chicks is short in the arctic summer, and early-hatched chicks may experience better growing opportunities if they hatch closer to the seasonal peak in food availability (Schekkerman et al. 2003). However, continuous incubation is not feasible for small shorebirds without jeopardising their own physical condition. The sandpiper species in this study spent on average 13-19% of the time off their nest. Such a short potential feeding time might impose energetic constraints to the birds, especially since incubating arctic shorebirds have a high energy expenditure (Piersma et al. 2003).

Under cold conditions, energy expenditure of incubating birds increases (Tinbergen and Williams 2002), whereas the availability of arthropod prey is strongly reduced (Schekkerman et al. 2003), which probably affects feeding success. Both factors may easily lead to a negative energy balance when feeding time is limited. Hence shorebirds may be expected to adjust their incubation behaviour at such times. In line with this, we found that weather significantly affected incubation scheduling and overall nest attendance in three of the four species studied. In the fourth (red phalarope), the small sample size is likely to be the reason for the absence of significant effects. Low temperature resulted in an increase in total recess
time. Such an increase was also found in the white-rumped sandpiper *C. fuscicollis* (Cartar and Montgomerie 1985), another uniparental arctic sandpiper. In contrast, nest attendance is more than 97%, irrespective of weather in the closely related but biparentally incubating dunlin and semipalmated sandpiper *C. pusilla* (Norton 1972; Cresswell et al. 2003).

Despite the increase in recess time at low temperature, LS and CS showed a negative correlation between body mass and temperature prior to weighing. Under the same conditions, cold periods did not lead to a reduced body mass in biparental dunlins. Our observations are therefore consistent with the notion that uniparental incubators experience energetic constraints as a result of a time allocation problem between incubation and feeding. This conclusion is further strengthened by our observation that little stints reduce mean recess length and total recess time in response to supplemental feeding (unpubl. data).

Except for a sudden drop coinciding with hatching of the eggs, average body mass does not decrease over the incubation period in little stints, suggesting that energy stores depleted during cold spells can be recovered when conditions improve (chapter 5). Little stints (and to a lesser extent other arctic sandpipers, Soloviev and Tomkovich 1997) carry considerable energy stores during incubation, enabling them to maintain high nest attendance even in prolonged cold periods. However, during or after some periods of particularly inclement weather, all of our study species except red phalaropes showed ‘long absences’ lasting up to eight hours. This indicates that this buffer does not always suffice and parents then prioritise their own condition. Although the sample of nests that survived to hatching was small due to high predation rate, all surviving nests that had experienced a ‘long absence’ hatched successfully, in one known case even when the long absence (4 h) took place two days before hatching. Viability costs of long absences may however be subtle and difficult to detect.

**Overall pattern in nest attendance: similar solutions between species**

Daily patterns of nest attendance were similar between the species studied. Most of the recesses were concentrated in the warmest part of the day, while recess length showed very little temporal variation except for the long continuous incubation sessions in the coldest hours. The length of these continuous incubation bouts increased in colder conditions, not due to an earlier start, but to a later end. Species did not differ in total daily recess time after correction for weather effects, though there was a clear tendency for small species (notably LS) to make more but shorter recesses than large species (notably CS).

The four species also showed remarkably consistent responses in incubation behaviour to variation in weather. In cold conditions, the number of recesses decreased, but recess length increased, so much that total recess time increased. In contrast, more but shorter recesses were made on rainy days.

Nest attentiveness (in relation to weather or egg/body size) has been described in many studies (e.g. for waders: Parmelee (1970); Norton (1972); Cartar and Montgomerie (1985); Løfaldii (1985); Cartar and Montgomerie (1987); Mehlum (1991); Delehanty and Oring (1993)) and was reviewed by Deeming (2001). The latter author did find a significant positive correlation between initial egg mass and nest attentiveness in birds, though over a much larger size range than covered by our study. Large eggs cool slower and could therefore be left unattended for longer periods than small eggs (Turner 2001), but cooling rate also depends on nest insulation (Reid et al. 2002). Both the composition and quantity of nest lining material differs between the four species in our study, the smaller ones having
better insulated nests (chapter 3). This may help explain the relatively small interspecific differences in incubation scheduling observed in our study.

Factors affecting the organisation of incubation

What can the similarities and differences between the four shorebirds species tell us about selection pressures on the organisation of incubation? Here we summarise several factors that may influence this organisation and predict how these are expected to affect length and number of recesses and their relationship with weather and body size. We then compare these predictions with our observations.

As both current and future reproductive success are jeopardised if the parents’ physical condition falls below a critical level, safeguarding sufficient food intake should be a priority. Therefore we expect that total recess time is maximised up to the level that is needed to fulfil daily energy requirements (DEE), and will increase with decreasing temperature and with rainfall (because DEE increases and intake rate decreases). In line with this prediction, we found that at low temperatures the total recess time increased, and that in or after some particularly bad periods, parents sometimes leave their clutch unincubated for long periods.

Within the constraints set by parental requirements, egg temperature should be maintained close to the optimum to allow optimal growth of the embryo and because reheating cooled eggs is energetically costly (Drent 1973; Biebach 1986; Hainsworth and Voss 2001; Turner 2001). In addition, movements to and from the nest may attract the attention of predators, and should thus be minimised. If only these factors would have to be taken into account, feeding should be concentrated in a single episode. However, we found that all species make many short recesses. This might be explained by the need to maintain egg temperature above a threshold for embryo development and the avoidance of digestive bottlenecks.

If embryos cease to develop below some threshold temperature (Webb 1987; Ewert 1992), long recesses will postpone hatching and increase exposure to predation, and should thus be avoided. In addition, if time allocated to feeding is limited by incubation demands, foraging efficiency should be maximised by avoiding digestive bottlenecks. When the digestive tract is full, the bird should stop foraging and incubate. Both considerations predict an incubation strategy with multiple short recesses, as was found in this study. They also both predict the observed pattern of shorter mean recess length in the smallest species (with fastest-cooling eggs and smallest stomach volume). However they make opposite predictions on relationships between recess length and weather. If maintaining egg temperature above a threshold is paramount, recess length may increase with ambient temperature as eggs cool slower, but should decrease during rain when they are likely to cool faster. If avoidance of digestive bottlenecks prevails and intake rate is weather-dependent, mean recess length should decrease at higher temperatures as stomachs are filled faster, but increase with rain as food availability declines (own obs.). In support of the first and contradicting the second argument is our finding that during rain all four species make more but shorter recesses. However, the increase in recess time on cold days is achieved through fewer but longer recesses, which supports the digestive bottleneck argument.

Foraging is energetically more expensive than incubating (Piersma et al. 2003), and going off the nest is only worthwhile when the energy intake during foraging outweighs the difference between energy expenditure during foraging and incubation. Thus we
would predict that foraging recesses are postponed during cold periods when energy expenditure during foraging is especially high, or expected intake rate is low. Indeed, during the coldest part of the day birds incubated continuously and this uninterrupted period of incubation became longer in poor weather.

The variation in findings supporting and/or contradicting the predictions regarding the organisation of incubation shows that no single factor can explain the whole pattern and overrides the importance of all others. We conclude that the observed incubation patterns reflect interactions between demands that sometimes conflict. The fact that some of these factors operate at different time scales means that direct trade-offs can sometimes be avoided. Due to the presence of energy stores in incubating birds, physical condition can be regulated within a time frame of several days, giving leeway for short-term adjustments to factors that may be critical over shorter periods, such as egg cooling rate.

**Incubation behaviour in relation to body condition**

During most of the time that we measured the attentive behaviour of the birds, we did not know their current physical condition. Energetic costs of incubation will affect parents in good and poor condition differently, and the level of their energy stores may influence time allocation decisions. This calls for an experimental approach in which either food availability, nest microclimate or the duration of the incubation period is manipulated while simultaneously monitoring physical condition and incubation behaviour of the parent (Reid et al. 2001). In two studies using supplemental feeding (Slagsvold and Johansen 1998; Gorman and Nager 2003), nest attentiveness increased. In a small-scale experiment in which we fed mealworms to little stints during incubation, birds also responded by reducing total recess time and recess length (unpubl. data). In response to experimental cooling of eggs Belding’s savannah sparrows *Passerculus sandwichensis beldingi* increased their attentiveness, while they decreased their attentiveness when eggs were warmed (Davis et al. 1984). Cresswell et al. (2003, 2004) experimentally reduced the energetic cost of heating the eggs in arctic shorebirds. As the incubating parent responded by sitting longer, they inferred that the ‘hunger level’ or energy store of the incubating bird determines the end of an incubation bout. Variation in body condition may thus be an important ‘hidden cause’ of the variability in nest attendance that remained unexplained in our analyses.
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References


Onder steltlopers komen allerhande gezinsvormen voor. Zo zijn er soorten waarbij de broedzorg netjes verdeeld is en beide ouders evenveel tijd aan het bebroeden van de eieren en de zorg voor de jongen besteden. Maar er zijn ook soorten waarbij één van de twee er alleen voor staat. Dat kan zowel het mannetje zijn, zoals bijvoorbeeld bij de franjepoten en de morinelplevier, als het vrouwtje, zoals bij de kemphaan en de krombekstrandloper. Kleine strandlopers doen het nog anders: het vrouwtje legt de eieren en dan gaat of zij, of de vader de eieren uitbroeden. De ander vertrekt en maakt een tweede legsel, waarschijnlijk meestal met een andere partner. Ook dat tweede legsel wordt door maar één vogel uitgebroed. Er zijn ook nog een aantal tussenvormen, waarbij het vrouwtje wel meehelpt met het uitbroeden van de eieren, maar er vandoor gaat zo gauw de kuikens er zijn. Bij nogal wat soorten wordt het uitslepende van de eieren en de opvoeding dus door maar één van de ouders gedaan.

Nu zijn steltlopers niet zo groot dat ze voordat ze met broeden beginnen zo veel reserves kunnen opslaan dat ze de hele broedtijd kunnen doorkomen zonder te eten. Ze moeten dus regelmatig om voedsel te zoeken. Maar op de koude toendra koelen de eieren erg snel af en als dat te lang duurt is het nadelig voor de ontwikkeling van de embryo’s. Waarschijnlijk moet de afwisseling tussen broeden en eten dus zorgvuldig gebeuren.

Om te onderzoeken hoe die afwisseling geregeld wordt, hebben we gemeten hoe vaak en hoe lang vier verschillende soorten met een éénoudersysteem het nest alleen laten. We hebben met behulp van kleine dataloggers continu de nesttemperatuur gemeten. Wanneer de ouder het nest verlaat zakt de temperatuur snel doordat de omgeving erg koud is en bij terugkomst stijgt hij weer tot de broedtemperatuur van bijna 40˚C. De soorten waarbij we dit gemeten hebben, kleine strandloper, rosse franjepoot, krombekstrandloper en gestreepte strandloper, broeden allemaal in hetzelfde gebied maar verschillen iets in grootte. Kleine soorten verliezen sneller warmte, doordat de oppervlakte van hun lichaam relatief klein is ten opzichte van de inhoud. Bovendien kunnen ze minder reserves opslaan dan grotere soorten. Daarom was onze verwachting dat de kleinste soorten het vaakst het nest zouden verlaten om voedsel te zoeken. Dat bleek ook zo te zijn. Verder gaan alle vier de soorten het vaakst en langst van het nest in de warmste deel van de dag. Ook al is
het 24 uur per dag licht, 's nachts koelt het toch aanzienlijk af en tussen 22u00 en 5u00 blijven ze meestal doorlopend op het nest. Overdag wisselen ze broedbeurten van ongeveer een half uur af met foerageeruitstapjes van zeven tot 15 minuten. Dat doen ze 22 tot 34 keer per dag en in totaal laten ze de eieren 3 tot 4,5 uur per dag alleen. Op koude dagen reageren alle soorten op dezelfde manier: ze gaan er minder vaak, maar langer af, waardoor de totale tijd die ze broedend doorbrengen korter is en meer tijd wordt besteed aan foerageren. Tijdens lange regenperiodes komen ze niet van hun nest af, maar als het slechte weer enkele dagen aanhoudt zie je soms dat ze voor zichzelf kiezen en de eieren urenenlang in de steek laten. Dat de eieren wel tegen een stootje kunnen, blijkt als deze legsels uiteindelijk toch gewoon uitkomen. Echt goed voor de eieren zal zo'n lange afkoelingsperiode echter niet zijn, alleen al omdat de broedperiode erdoor wordt verlengd. We hebben niet gemeten of eieren van alleen broedende soorten beter bestand zijn tegen de kou dan eieren van soorten waarbij beide ouders broeden, maar het is denkbaar dat dit zo is.

De meeste steltlopersoorten hebben in de tijd dat ze eieren uitbroeden een klein voorraadje vet, dat ze kunnen aanspreken als ze door slecht weer het nest niet kunnen verlaten. Steltlopers die alleen broeden zullen deze voorraad sneller moeten aanspreken dan soorten waarbij beide partners helpen, omdat ze minder tijd hebben om te foerageren. Dat patroon zien we terug in de verzamelde gewichtsgegevens. Terwijl kleine strandlopers en krombekstrandlopers gewicht verliezen als het enkele dagen achtereen koud weer is, blijft het gewicht van bonte strandlopers, waarbij mannetje en vrouwtje afwisselend broeden, gewoon op peil. De energievoorraad van de alleenstaande ouders stelt ze dus in staat om op koude dagen toch veel tijd op het nest te kunnen doorbrengen, zodat de eieren niet te vaak of te veel afkoelen.