

RIJKSUNIVERSITEIT GRONINGEN

The arctic pulse

Timing of breeding in long-distance migrant shorebirds

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Contents

1. Introduction	8
2. Body condition of shorebirds upon arrival at their Siberian breeding grounds	32
Ingrid Tulp, Hans Schekkerman, Raymond Klaassen, Bruno Ens and G. Henk Visser † <i>Submitted</i>	
3. Eggs in the freezer: energetic consequences of nest design in tundra breeding shorebirds	54
Ingrid Tulp, Hans Schekkerman and Joep de Leeuw <i>Unpublished manuscript</i>	
4. Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule	74
Ingrid Tulp and Hans Schekkerman <i>Published in 2006 in Journal of Avian Biology 37: 207-218</i>	
5. Body mass patterns of little stints at different latitudes during incubation and chick-rearing	98
Ingrid Tulp, Hans Schekkerman, Przemek Chylarecki, Pavel Tomkovich, Mikhail Soloviev, Leo Bruinzeel, Klaas Van Dijk, Olavi Hildén †, Hermann Hötker, Wojciech Kania, Marc Van Roomen, Arkadiusz Sikora and Ron Summers <i>Published in 2002 in Ibis 144: 122–134</i>	
6. Energetic and time-budget consequences of incubation and chick-rearing in high arctic breeding shorebirds: what is the most demanding phase?	120
Ingrid Tulp, Hans Schekkerman, Leo W. Bruinzeel, Joop Jukema, G. Henk Visser † and Theunis Piersma <i>Submitted</i>	
7. Growth and energetics of a small shorebird species in a cold environment: the little stint <i>Calidris minuta</i> on the Taimyr Peninsula, Siberia	144
Kathy Tjørve, Hans Schekkerman, Ingrid Tulp, Les G. Underhill, Joep de Leeuw and G. Henk Visser † <i>In press (Journal of Avian Biology)</i>	
8. Correlates of growth rates in arctic shorebird chicks: daily weather and food abundance	168
Ingrid Tulp and Hans Schekkerman <i>Unpublished manuscript</i>	

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9. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation	190
Ingrid Tulp and Hans Schekkerman	
<i>In press (Arctic)</i>	
10. General discussion	216
Samenvatting	241
Authors addresses	252
Tot slot	254

Chapter 1



Introduction

Timing of breeding

Reproductive success in relation to variation in timing of breeding has been studied in many bird species, and especially the hypothesis that timing of breeding is tuned to food availability, has received a lot of attention (Lack 1968; Perrins 1970; Daan et al. 1989; Brinkhof 1995).

Lack (1950) proposed that on average breeding is timed so that the hatching of chicks coincides with the peak in food supply. Later Perrins (1970) showed that in at least two species most individuals breed later than would be expected based on the optimal timing for chicks. He concluded that an earlier timing was constrained by the proximate mechanism of a food shortage for the female at the time when eggs need to be produced. This led to experimental studies where females were experimentally supplied with extra food. In a recent review Drent (2006) summarized the findings of ten such studies and he concluded that supplemental feeding led to only a slight advancement of egg-laying. Apparently there are other factors, possibly controlled by an internal rhythm, that play a role as well. Studies in which laying date was advanced experimentally did result in higher reproductive output, but at the cost of reduced parental survival. The timing of breeding is therefore the result of a compromise between the best chances both for survival of the chicks and the adults. The conclusion is that laying date is optimised on the individual level influenced by local environmental conditions (Drent and Daan 1980; Daan et al. 1989; Brinkhof 1995; Daan and Tinbergen 1997).

The Arctic as a magnifying glass?

Most environments on earth are not constant but show variation in day length, weather and food availability depending on the time of year. Opportunities for successful reproduction are therefore limited and restricted to a limited period per year (Alerstam 1990).

Many shorebird species are long distance migrants that spend the nonbreeding season at temperate or tropical latitudes and undertake migrations to their arctic breeding areas in spring. Timing of breeding in long-distance migratory shorebirds is closely linked with other parts of the annual cycle. Most species have a tight time schedule within which they travel from their wintering sites, through stopover sites to the breeding areas (Piersma 1987; Ens et al. 1994). The onset of breeding is often only days after arrival at their arctic breeding sites.

The Arctic may stand out from temperate regions because of its extremes in environmental forcing. Arctic areas are not inhabitable for the greater part of the year by most organisms unless they have developed certain adaptations to overcome the limits set by the harsh environment (Scholander et al. 1950; Morrison 1964; Andrews and Ryan 1971; Wang et al. 1973; Giardina et al. 1989; Brix et al. 1990; Stokkan 1992). Snow covered, with temperatures far below freezing and without daylight for most of the winter: certainly circumstances that do not make an easy living. As evidenced by ptarmigan *Lagopus mutus*, snowy owl *nyctea scandiaca*, snow hare *Lepus timidus* and lemmings it is nonetheless possible to live here year round (Wang et al. 1973; Chernov 1985; Stokkan 1992; Reid and Krebs 1996). But without their abilities to find food and shelter below the snow and adaptations to withstand the low temperatures, they would not be able to survive. The Arctic is therefore not an environment where shorebirds can stay year round. With their sensitive bill tips they need soft sediments or vegetation to look for food (Piersma et al. 1998). The logical consequence then is to migrate away from the place of birth or the breeding site in the arctic tundra and spend the rest of the year in areas that do provide the necessary conditions for survival.

The arctic summer is short and time available for finding a mate, laying eggs, raising chicks and preparing for migration is hardly more than two months. Even within this period, weather is capricious, with large day-to-day variations in temperatures and regular occurrences of strong winds, rain and snow showers. In addition, food abundance (arthropods) shows a seasonal peak and strong weather-dependence. Therefore, arriving on time and in a condition that allows a quick start of breeding may be paramount for successful reproduction. This does not necessarily mean that the relevance of an appropriate timing is stronger here or that birds are more time stressed here than in more temperate systems. Although it has been the general conviction that the relevance of an appropriate timing increases with climate harshness, there's increasing evidence that also in temperate climates the season with the right conditions for reproduction is short (Both et al. 2006). The length of period in which food conditions are sufficient for successful breeding and the energetic requirements caused by local environmental conditions are relatively low, is what determines the size of the window of opportunity (figure 1.1). The seasonal pattern in food abundance will depend on the type of food and the way the environment interacts with its availability. The part of the window of opportunity that is determined by food abundance is less likely to differ greatly between temperate and arctic sites. Energetic requirements however show the steepest decline and largest difference between winter and summer months in arctic areas (Wiersma and Piersma 1994). This aspect is different from temperate areas: here the opportunities for successful reproduction are predominantly limited by food availability, whereas the seasonal effect on energy requirements show less steep changes than in the Arctic. Whereas in the Arctic many species depend on arthropod fauna as a single food source, in temperate areas there are often more alternatives. Another aspect that differs from temperate zones is the huge short-term variation in weather. In midsummer cold spells lasting several days are not uncommon and even within a day temperatures can easily vary over more than 10°C. Because of the general lower temperature level, such fluctuations have high impacts. A drop from 10 to 2°C has a stronger effect than a drop from 25 to 17°C. For instance, the availability of arthropods can vary by a factor 5 between consecutive days.

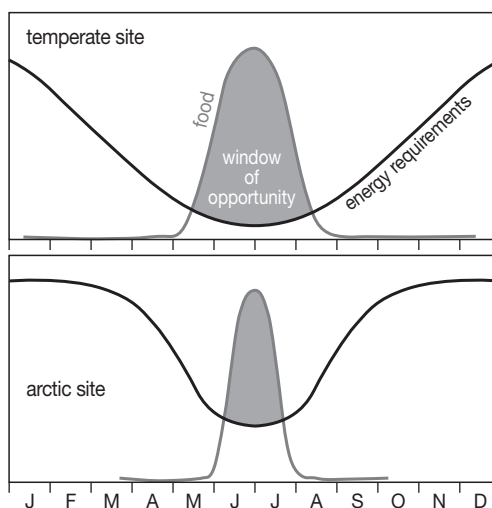


Figure 1.1. The presumed window of opportunity for shorebirds breeding at a temperate (upper) and arctic (lower) site. The black line indicates the seasonal pattern in energetic costs, the dotted line the seasonal pattern in food abundance.

Consequently, processes related to timing of breeding in the Arctic may be as if observed through a magnifying glass. In addition, of all climatic zones on earth, arctic areas have shown the greatest climatic change in the past decades (Meehl et al. 2005). In line with this, predicted effects of climate change are expected to show up most prominently in the Arctic (McBean 2005).

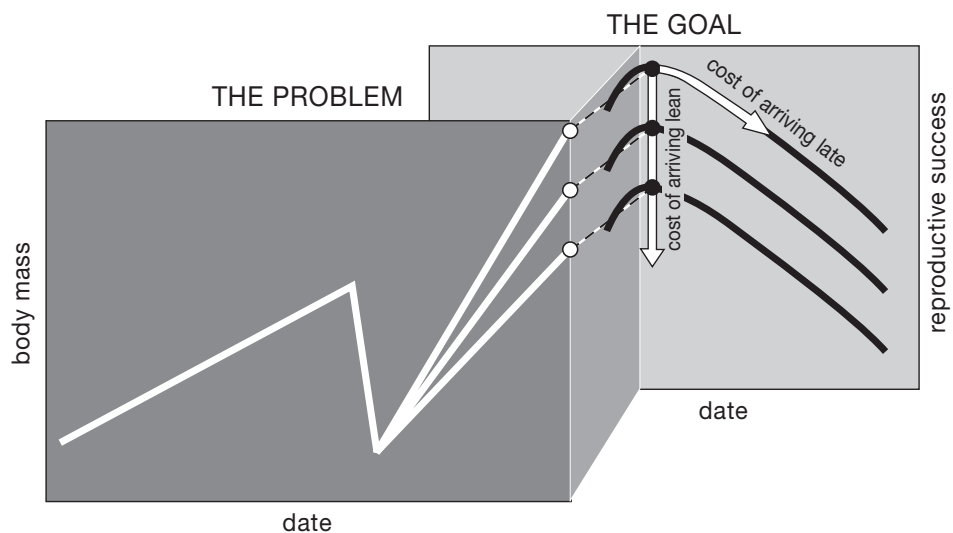
For the moment, neglecting the question what brings shorebirds to the Arctic in the first place, the central theme of this thesis is: what are the selective forces that determine the timing of breeding of arctic breeding shorebirds?

The breeding season in the annual cycle: the terminal reward

Another special feature of the Arctic is that most species that breed there come from far away. So, there is not only the decision to be made of when to start breeding, but also of when to leave the wintering grounds and when to arrive on the breeding grounds. Models of bird migration have tried to describe the annual cycle including migration and breeding.

The basic assumption in these models is that there is a relationship between arrival date and arrival condition and breeding success, as a proxy for fitness (Ens et al. 1994; Weber et al. 1998). Yet, in contrast to the situation in arctic breeding geese (Ebbinge and Spaans 1995; Madsen 2001), to date there is little direct published evidence of such a relationship in shorebirds. The models assume that reproductive success has an optimum with respect to arrival date, or declines continuously to some final date beyond which reproduction is impossible (figure 1.2). Furthermore, some minimum condition is required to initiate a clutch. Both arrival date and condition may be influenced by factors operating in the wintering areas and at migration stopovers (site quality) or during migratory flights (weather), and they may determine whether there is enough time to raise chicks before the end of the summer, or the number and quality of eggs being produced. The shape of this 'terminal

Figure 1.2. Schematic presentation of the link between maximizing reproductive success and the time and body mass at arrival on the breeding grounds (from Ens et al 1994).



reward function' is based on general patterns in birds, but varies between species, localities, and years. The project set out to collect data on the breeding grounds to provide an empirical basis for these models of migration for shorebirds. This model can then be used to evaluate the effect of (human-induced) disturbances to the optimal migration schedule (Weber et al. 1999).

Approach

The original approach of this study was to measure reproductive success in shorebirds in relation to arrival date and condition. We wanted to capture birds upon arrival to have accurate measures of both arrival date and arrival condition and follow their breeding performances. In practice, this did not work. Only few of the birds captured upon arrival stayed within the study area, predation rates were high and estimating fledging success in most species was not feasible. In a more indirect approach we did measure the seasonal pattern of food availability and compared this with energetic demands and performance of parents and young (energy expenditure, condition, growth, time available for foraging). The rationale behind this is that if we can pin down energetically stressful periods, it may be possible to identify selection pressures on the timing of breeding. Additional insight can then be gained by comparing the findings among species that have different reproductive strategies.

Factors that may be important for timing of breeding

Conditions at arrival and in the pre-laying phase.

The risk of starvation upon arrival is probably the greatest potential cost of being early. On the other hand, early arrival may bring several benefits. Early birds may obtain the better territories with respect to food supply or safety. Arrival date may also affect the options to choose a mate, including the chance to remate with a known partner, as in the black turnstone *Arenaria melanocephala*, where reunited pairs fledged more young than newly formed pairs (Handel and Gill 2001). Early arrival may also translate to an early laying date, although variation in the time needed to accumulate nutrients for egg production may modify this relationship. Early arriving birds may be able to prepare their body for breeding faster if they have access to better feeding sites (Morrison et al. 2005), though arctic waders often feed outside their breeding territory. However, laying date can also be constrained by a late snowmelt. Because nests in small snow-free patches incur a high predation risk (Byrkjedal 1980), eggs can only be laid once suitable nesting ground is exposed (Green et al. 1977).

Food availability for chicks.

Abundance of surface-active arthropods that form the main food of arctic wader chicks, generally peaks during a short period in (most often) July, the timing of which varies under the influence of weather conditions. A hatching date well-timed to the insect peak will increase chick growth rate and survival (Schekkerman et al. 1998a). Although some early authors identified hatching as the phase to be matched with the insect peak (e.g. Nettleship 1973), this may not be the whole story, as required foraging intake rates are higher for older chicks with their greater energy requirements (Schekkerman et al. 2003).

Food availability for adults during incubation.

Although adult waders may utilise a wider food spectrum than chicks (e.g. also buried larvae), food availability for them may also be highest during the peak of surface arthro-

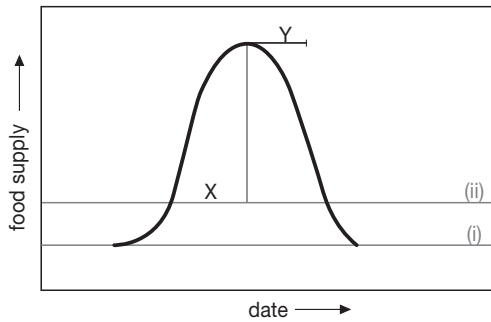


Figure 1.3. Hypothetical relationship between food supply, date of laying and date of young becoming independent. The curve shows level of food abundance against (i) the food required for general body maintenance and (ii) the food required for forming eggs. The straight line X represents the time required for forming and laying eggs and incubating these to the point of hatching. Line Y represents the time taken to raise the young to the point of independence (from Perrins 1970).

pod activity. This may lead to a conflict of interest between adults (which could alleviate energetic problems by incubating during the insect peak) and chicks (which should have hatched by then, figure 1.3).

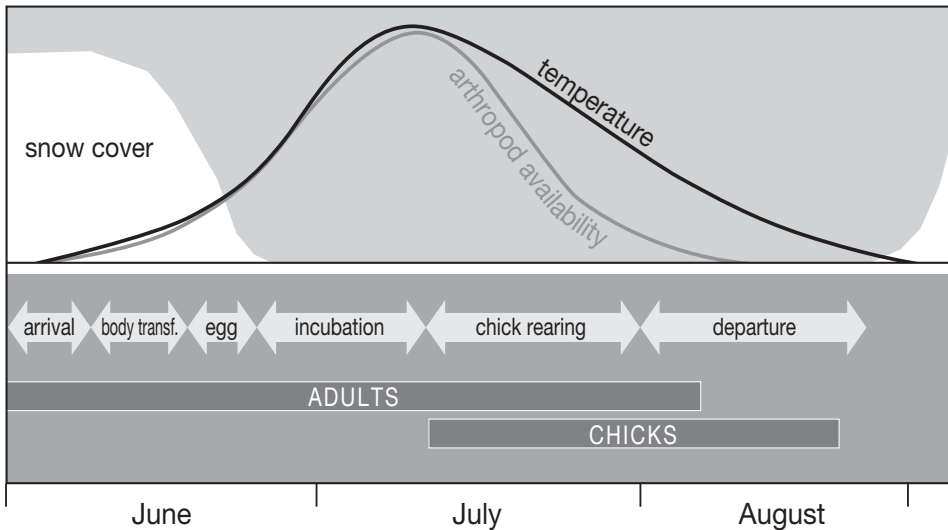
Energy needs throughout the breeding season.

Mean air temperature varies from below the freezing point when shorebirds arrive, to as high as 25°C in mid summer. But weather can be highly variable from day to day. Even in mid summer, days with low temperatures and snow or rain showers occur. Walking around on the windswept tundra generally costs more energy than sitting tight in a nestcup sheltered from the wind (Piersma et al. 2003). Most shorebirds are precocial: they have self-feeding chicks. Unlike adult birds, young chicks are incapable of maintaining their body temperature (Visser and Ricklefs 1993; Krijgsveld et al. 2001). Therefore young chicks require regular brooding by their parents to enable their body temperatures to increase. As a result, the time budget of the parents is limited by the time needed for brooding. The organisation of the breeding cycle – what activity takes place in which period – will define the energy needs throughout the season and may affect the optimal timing of breeding (figure 1.4). Also in this respect the interests of parents and chicks may differ with regard to timing of hatching.

Competition during autumn migration.

In many shorebird species, one parent deserts the breeding area well before the chicks have fledged, and even the remaining parent usually migrates away before the young (Cramp and Simmons 1983). This may reflect a declining food supply in the tundra, but may also point to some advantage of arriving early at autumn staging or moulting sites. An indication for such an advantage is the study of Boates and Smith (1989), who found that in response to the influx of migrant semipalmated sandpipers *Calidris pusilla* into the Bay of Fundy in late July, the larger male amphipods *Corophium volutator* did not show up at the surface anymore due to a behavioural shift and depletion by sandpipers. Thus only the early-arriving birds can take advantage of the most profitable prey. There are several other examples of prey depletion at autumn staging sites (Schneider and Harrington 1981; Szekely and Bamberger 1992; Zwarts et al. 1992).

Figure 1.4. Shorebirds breeding in the Arctic are dealing with a season that is limited to 2.5 months. In spring nesting can only start once the snow has disappeared, while food and temperature show a strong seasonal pattern. The bars indicate the periods when adults and chicks are present in the area.



Parental care systems

Many systems of parental care exist in shorebirds. Apart from the biparental system in which both parents share incubation and chick-rearing duties, a variety of systems occur with unbalanced parental roles (Reynolds and Szekely 1997). At the extreme of these, the contribution of one sex is reduced to fertilization only (as for example in ruff *Philomachus pugnax*, van Rhijn 1991). This might even take place already during a stopover on northward migration. Shorebirds are also known for the occurrence of reversed sex roles. In that case the contribution of the female is reduced to egg laying but she leaves the remaining the parental duties to the male, as is the case in phalaropes (Schamel 2000). The consequence of both these examples is that one bird carries out all parental duties alone ('uniparental'). However, also within biparental systems variations occur. Some species take care of eggs and chicks together until the chicks fledge, while in others the male or the female leaves when the eggs hatch or shortly after that.

The different parental care systems have great consequences for the energy and time budgets of parents. For instance, birds that share incubation and chick-rearing duties will have more time available for feeding than birds that fulfill all parental duties alone. In the Arctic, species representing several of this array of parental care systems co-occur. This provides a unique opportunity to investigate constraints on breeding as the different systems affect time-energy budgets differently.



Figure 1.5. Location of the study area (circle near Dikson) on the Taimyr Peninsula.

Study area

The majority of the studies presented here are based on fieldwork that was carried out in 2000-2002 at Medusa Bay situated 18 km south of Dikson in the west of the Taimyr peninsula, Siberia, Russia ($73^{\circ}20'N$ $80^{\circ}30'E$, figure 1.5). In some chapters in the thesis I also use data that were collected in 1996 by an expedition under the umbrella of the Working Group for international Waterbird and Wetland Research (WIWO). In one chapter (chapter 5) a compilation of data is used that were collected in different locations across the Siberian Arctic by many teams of researchers in different years.

In 1994 the Dutch Ministry of Agriculture, Nature Management and Food Safety financed the building of a field station at Medusa Bay to stimulate research in the area as well as co-operation between Russian and Dutch scientists. Gerard Boere, at the time working at the ministry, was the driving force behind this. Our studies were funded by the Dutch Ministry



of Agriculture, Nature Management and Fisheries (DWK program 404). The precondition for this study was that we would base ourselves at this field station. This was not entirely a logical choice considering the conservation-oriented scope of the work and the desired emphasis on species for which the Wadden Sea is an important stopover site. Most of the species that breed in Medusa Bay either do not follow the East Atlantic Flyway, but follow a more eastward route (dunlin, Pacific golden plover), or, if they do use the East Atlantic Flyway, hardly use the Wadden Sea (little stint, curlew sandpiper). The Wadden Sea species are generally found further north and east in Taimyr, places that are much harder to access than Medusa. Nevertheless, given the practical problems included in working in remote areas such as the Siberian Arctic, the availability of a field station provides an opportunity that must not be underestimated. Furthermore, the problems encountered by arctic breeding shorebirds are unlikely to depend on longitude.

At the latitude of Medusa Bay there is continuous daylight throughout the breeding period. The last sunset is on 3 May and the first sunset on 11 August. Medusa Bay is situated at the northeastern end of the river Yenissei, near the mouth (figure 1.5). The field station is situated on the northeast side of the bay, on a small peninsula. Most of the shorebird breeding biology studies were undertaken in a 4 km² area east of Medusa Bay, bounded by natural borders: the Medusa river in the south, the bay and the sea in the north and west and another small river in the northeast (figure 1.6).

The study area can be classified as 'arctic tundra' according to (Chernov 1985), with some characteristics of 'typical tundra'. This somewhat vague terminology is used for the area that stretches out between the July 8-11°C isotherm in the south and 1.5°C isotherm in the north. The vegetation is low, without trees and bushes and usually not higher than 30 cm. Arctic tundra is characterized by patches of bare ground, which are often surrounded by fringes of vegetation. This type of polygonal tundra is formed by frost heaving and stretches of it are present at Medusa Bay. Other features caused by the action of frost and thawing are noticeable everywhere: split blocks and stones, cracks in the ground and mounds. In summer the landscape is colourful because of the abundance of flowering plants, especially on south slopes.

At Medusa Bay the landscape is characterised by a rolling relief. The top of the highest hill in the intensively studied area is situated 39 m above sea level, and the lowest point is at sea level. No lakes or ponds are present. To the east of the study area the relief becomes more distinct, with hilltops reaching as high as 160 m above sea level. Rock formations are



present throughout the area and rocky outcrops are often found on steep slopes. Gravel occurs along rivers, at river mouths and on beaches. The vegetation consists of lichens, mosses, sedges, grasses, dwarf willows *Salix polaris*, and various herbs on the slopes and plateau's on top of hills. In the marshy areas found in valleys, on the lower parts of slopes and sometimes on hilltops, extensive meadows of sedges *Carex* spp. predominate. East, north and southeast of the plot large polygonal bogs are found. In most of the area well-vegetated tundra predominates, with few areas of frost-boiled tundra with clay-medallions. Part of the area is traversed by tracks of caterpillar vehicles, which has changed the landscape considerably. In these tracks vegetation cover increases through proliferation of grasses and sedges. Also tracks cause drainage and creation of micro-relief and new puddles. Some shorebird species seem to prefer these tracks for nesting.



Generally mean daily temperatures increase to above 0°C and snow starts to melt in the first half of June, and in early September mean temperatures tend to drop below 0°C and the first permanent snow occurs (NCDC Climate Resources, www.ncdc.noaa.gov).

In the years 2000 and 2001 few lemmings were around, while numbers were on the increase in 2002, although densities usual in 'lemming peak years' (such as 1996) were not reached (www.arcticbirds.ru). Only in 1996 and 2002 numbers were high enough to encourage predators such as snowy owls *Nyctea scandiaca* and pomarine *Stercorarius pomarinus* and long-tailed skuas *S. longicaudus* to start nesting, although these species did suffer problems in finding enough lemmings to feed their mates and chicks later in the season. In all years arctic foxes *Alopex lagopus* were present in the area, leaving behind a trace of empty wader nests, especially in 2000 and 2001. In 2002, arctic fox numbers had been much reduced by two years of lemming scarcity, foxes were present in the surroundings and visited our study area a few times. Nevertheless, predation pressure on breeding waders was noticeably less in 2002 than in 2000 and 2001, and good numbers of chicks hatched.



In order of decreasing breeding density the local shorebird community consists of little stint *Calidris minuta*, Pacific golden plover *Pluvialis fulva*, dunlin *Calidris alpina*, curlew sandpiper *Calidris ferruginea*, ringed plover *Charadrius hiaticula*, turnstone *Arenaria interpres* and Temminck's stint (table 1.1). In some years red phalarope *Phalaropus fulicarius*, dotterel *Charadrius morinellus*, pectoral sandpiper *Calidris melanotos* and ruff *Philomachus pugnax* bred in the area as well. In years with high lemming peaks (1996, 2005) brent geese form colonies around nests of snowy owl (Tulp et al. 1997; van Kleef et al. 2007). Other species that breed in the area (in some years) include several duck and passerine species (table 1.2).

Table 1.1. Numbers of shorebird nests and broods of which nests were not found, inside the 4 km² intensive study area in 1996 and in 2000-2002. The last column shows in which chapters the different species are featuring.

species	nests + broods in 4 km ²				chapter
	1996	2000	2001	2002	
little stint <i>Calidris minuta</i>	74	110	94	99	2, 3, 4, 5, 6, 7, 8, 10
dunlin <i>Calidris alpina</i>	13	31	18	20	2, 3, 4, 6, 8, 10
Pacific golden plover <i>Pluvialis fulva</i>	23	27	26	17	3, 10
curlew sandpiper <i>Calidris ferruginea</i>	71	13	19	10	2, 3, 4, 10
ringed plover <i>Charadrius hiaticula</i>	6	10	2	6	10
ruddy turnstone <i>Arenaria interpres</i>	5	3	2	4	2, 3, 10
red phalarope <i>Phalaropus fulicarius</i>	-	-	2	3	2, 3, 4, 10
pectoral sandpiper <i>Calidris melanotos</i>	-	-	7	2	4, 10
Temminck's stint <i>Calidris teminckii</i>	-	1	2	1	
ruff <i>Philomachus pugnax</i>	1	-	1	-	
dotterel <i>Charadrius morinellus</i>	-	-	2	-	2

Table 1.2. Numbers of nests of other species, inside and outside the 4 km² intensive study area (but within the area shown in figure 1.6) in 1996 and in 2000-2002.

species	nests inside + outside 4 km ²			
	1996	2000	2001	2002
brent goose <i>Branta bernicla</i>	51	-	1	12
white-fronted goose <i>Anser albifrons</i>	-	-	1	-
long-tailed duck <i>Clangula hyemalis</i>	-	-	-	1
Steller's eider <i>Polysticta stelleri</i>	-	-	-	1
king eider <i>Somateria spectabilis</i> (brood)	-	-	-	1
ptarmigan <i>Lagopus mutus</i>	-	4	4	5
long-tailed skua <i>Stercorarius longicaudus</i>	3	-	3	4
pomarine skua <i>S. pomarinus</i>	4	-	-	18
snowy owl <i>Nyctea scandiaca</i>	4	-	-	2
rough-legged buzzard <i>Buteo lagopus</i>	3	1	-	-
shorelark <i>Eremophila alpestris</i>	12	6	14	7
red-throated pipit <i>Anthus cervinus</i>	1	2	6	1
white wagtail <i>Motacilla alba</i>	-	1	1	-
northern wheatear <i>Oenanthe oenanthe</i>	-	-	1	1
common redpoll <i>Carduelis flammea</i>	-	-	-	1
Lapland bunting <i>Calcarius lapponicus</i>	7	18	15	10
snow bunting <i>Plectrophenax nivalis</i>	3	23	9	6

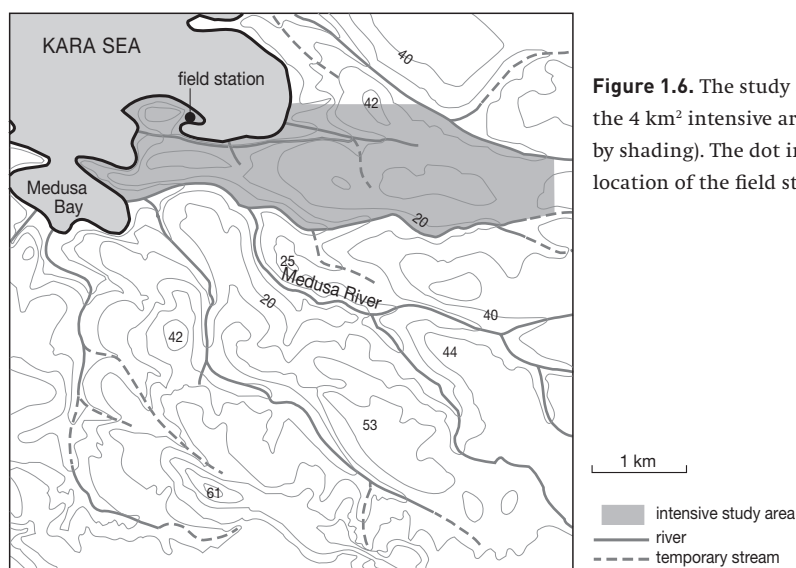


Figure 1.6. The study area, with the 4 km² intensive area (indicated by shading). The dot indicates the location of the field station.

Study species

There are several species featuring in this thesis (table 1.1). To avoid repetition of descriptions of the characteristics of the main species, here I will introduce the ones that play a major role. Their order reflects their importance in the thesis.

Little stint

Little stints have a wide distribution in winter, ranging from the Mediterranean in the north all along the African east and west coast, as far south as South Africa and as far east as India (Cramp and Simmons 1983, figure 1.7). In the Arctic little stints are also widespread and locally very abundant. The breeding area ranges from northern Scandinavia in the west to east Russia, beyond the Lena Delta in the east. Little stints are not faithful to their breeding site. In 2000-2002 we ringed 582 full-grown little stint, of which half were colour-marked and we ringed 320 chicks, but never saw a single one again. Nor did we ever resight any of the 67 colour-ringed adults and 75 ringed chicks that were ringed in 1996. Despite thousands of birds having been ringed in both in Taimyr and abroad, only very few Taimyr little stints have been recovered elsewhere. We received three recoveries from our colour-marked birds from wintering areas in Namibia, Tanzania and Israel (figure 1.7).

As an unbiased scientist you're not supposed to have favorites but I can't help that for me little stints are the absolute champions among arctic breeding shorebirds. Apart from being the smallest shorebird in the Siberian Arctic, they also take care of the eggs and chicks alone. The female lays a clutch of four, after which one of the parents (usually the male) starts incubating this clutch, while the female moves further north and produces a second clutch, likely with another male (Hildén 1978; Tomkovich et al. 1994; Tulp et al. 2002). Starting with a mere 4 g, the tiny fluff balls on their enormous legs grow at high speed to full-sized birds in little over two weeks. Furthermore, little stints are extremely enjoyable to work with due to their tameness. They will readily keep the chicks warm while you take chick by chick to ring and measure them, after which you put them back under

the parent's belly! The repertoire of tactics they use to lead you away from nest or chicks is extensive and very charming to a human observer (although definitely not intended like that). Perhaps one of the most striking is the one we called the "dead sheep display" where the bird sits behind a tussock and jumps vertically into the air, while squeaking like a lemming (something that reminded us of the dead sheep falling from the sky featuring in one of the Monty Python movies). They generally breed in the wetter areas along streams, in sedgefields and polygonal tundra. This is also the area where they stay once the chicks are born. Young chicks are reasonably easy to work with, but they tend to become more difficult to track when they grow older and no longer require brooding.

Dunlin

The subspecies breeding in Taimyr is *Calidris alpina centralis* (Engelmoer and Roselaar 1998). The nonbreeding area of this subspecies is largely unknown; there have been only two recoveries of birds ringed in eastern Taimyr from the Sivash (Sea of Azov in the Black Sea area) in 2003/2004 (P.S. Tomkovich pers. comm.). The most likely wintering area is somewhere in the Persian Gulf (figure 1.7). We also never got a single recovery from the 150 adult dunlin that we ringed and (part of them) colour-marked in our study area, nor from the 136 birds ringed as chicks. Together with Pacific golden plover and ringed plover, dunlin is the only site-faithful species in the area. We systematically colour-marked all dunlin breeding in the area and based on three years data we calculated an apparent annual survival rate of 69% (Schekkerman et al. 2004). Dunlin are biparental during the egg phase. Male and females take equal turns in incubation, but as soon as the chicks hatch the female leaves. She is often still seen for a few days in the area, but not near the nest and leaves shortly after. Dunlin breed in wet areas, often in tracks produced by caterpillar vehicles. They often breed very close to the nest site of the previous year. The chicks are notoriously difficult to find because of their behaviour and their extremely good camouflage.

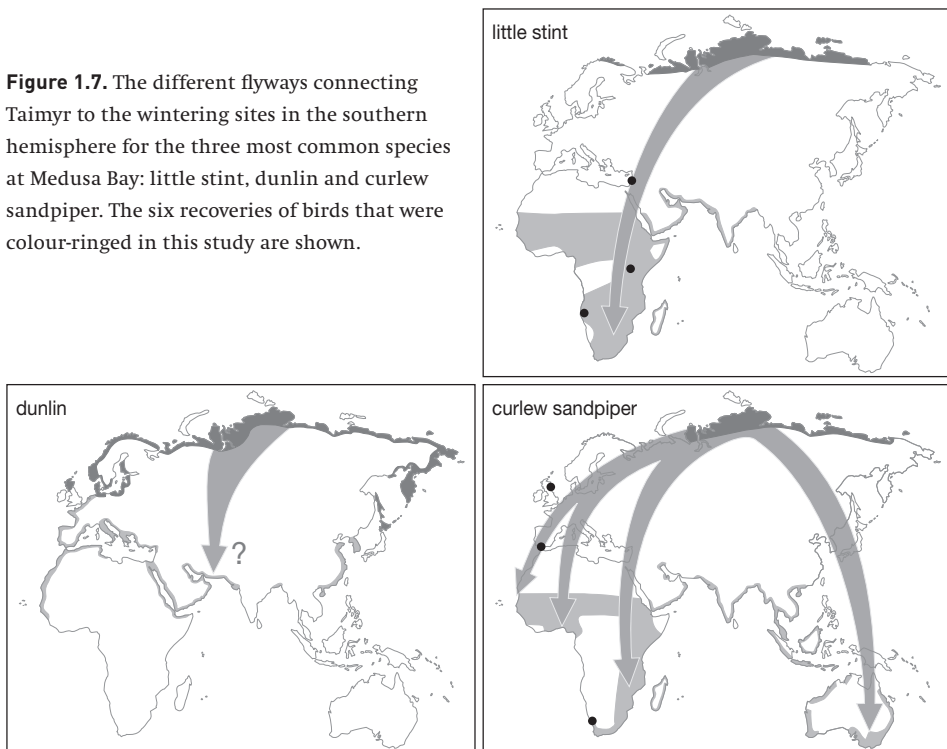
Curlew sandpiper

The curlew sandpiper is a breeding bird of the arctic tundras in northern Siberia between the Yamal Peninsula in the west and the Chuckchi Peninsula in the east (Lappo and Tomkovich 2006). They spend the nonbreeding season at southern latitudes from sub-Saharan Africa to New Zealand (figure 1.7). It is a strictly uniparental species; the male leaving after the



eggs are produced and even chased away from the territory by the female. Males leave the breeding area early in the season and are seen on southward migration in the beginning of July in the Wadden Sea (Bijlsma et al. 2001). Curlew sandpipers are not breeding site-faithful. None of the 37 (2000-2002) and 43 (1996) colour-ringed adults or 45 (2000-2002) and 72 (1996) ringed chicks returned to the breeding site in the years of study. Curlew sandpipers ringed at Medusa Bay were reported from Britain, Spain (ringed as chick) and South Africa, all in autumn. They breed in the area every year, and in some years in extremely high densities (1996, table 1.1). Curlew sandpipers nest in the drier parts of the area, often on hill slopes. With chicks they move towards the wetter valleys (Schekkerman et al. 1998b) and are very difficult to find when they are older than a few days of age.

Figure 1.7. The different flyways connecting Taimyr to the wintering sites in the southern hemisphere for the three most common species at Medusa Bay: little stint, dunlin and curlew sandpiper. The six recoveries of birds that were colour-ringed in this study are shown.



Outline of the thesis

The different chapters in the thesis follow the arctic summer in a chronological order. Although this is not the order in which they were originally written, this seems the most logical way of presenting them and provides the best possibilities to build the next paper on the findings of previous ones.

Arriving in the snow

The body condition with which shorebirds arrive from their last spring stopover site in the Siberian Arctic is still largely undescribed (but see Morrison et al. (2005) for red knot *Calidris canutus* in northernmost Canada). The expectation is that most of the energy stores are depleted after the long distance flights into the breeding areas. Empirical studies have confirmed that arctic shorebirds generally produce eggs not from nutrients brought from the wintering grounds but from nutrients collected after arrival on the breeding grounds (Klaassen et al. 2001; Morrison and Hobson 2004). However, a residual store could still be of use if it can provide some leeway in case they find a snow covered tundra upon arrival without feeding possibilities (Morrison and Hobson 2004). The reason for the lack of information on arrival condition is that usual methods for catching birds, such as mist netting, do not work in the Arctic because of continuous daylight. Also situations that would enable the use of cannon nets such as communal roosts or feeding sites do not occur much (with the exception of Alert, see Morrison et al. 2005). Therefore we used a modified version of the wilsternet (a clap net used for catching golden plovers in The Netherlands, Jukema et al. 2001) that is successful in catching migrating waders in stopover and wintering areas but was hitherto never applied in the arctic breeding areas. In chapter 2 we describe arrival condition both in terms of total body mass, and by means of the deuterium dilution method also in terms of lean and fat mass.

Warming eggs on the icy tundra

Upon arrival, the tundra is still snow covered and frozen. The permafrost layer is only centimeters away from the surface. Since in some species egg laying starts within days upon arrival, it means that in practice they have to lay their eggs on frozen ground. Not a very energy-efficient place, considering that eggs need a high and constant temperature for successful embryonic development (Drent 1975; Webb 1987). The way shorebirds protect their eggs against the cold environment through careful nest design is the subject of chapter 3.

Time problems of single parents

Many species at the study site take care of eggs and chicks alone. Since shorebirds do not build up enough stores to sit out the incubation period, they have to leave the nest at regular intervals to feed. Time allocation during incubation is likely to depend on factors influencing egg cooling rates as well as parental energy requirements and food intake rates. The co-occurrence of four uniparental species that differ in size (little stint, red phalarope, pectoral sandpiper and curlew sandpiper), provided an excellent opportunity to study how different species deal with this time allocation problem. Using small data-loggers that registered the temperature in the nest we compared incubation rhythms between these species and investigated weather effects on the organisation of incubation in chapter 4.

Extra's for bad times

The energetic consequences of a uniparental lifestyle was the topic treated in chapter 5, with little stint as the model species for which a wealth of information on body mass dynamics was collected by 17 expeditions to 12 sites by over 30 people between 1976 and 1998. Mass stores in birds can serve as an insurance for transient periods of negative energy balance, but carrying such stores entails certain costs as well. Therefore, body mass may vary in relation to climatic conditions and stage of the breeding cycle. The compilation of data all over the Arctic allowed us to investigate how body mass varies with latitude and stage of breeding.

The housekeeping book of single parents

Energy expenditure during incubation is much higher for arctic breeding shorebirds than for their temperate congeners due to the colder environment (Piersma et al. 2003). High energy expenditure can only be compensated by high energy uptake through increased food intake. Especially in uniparental species an increased food intake might be difficult to accomplish within the limited time that is available for feeding. In addition food may also not be superabundant. Once the chicks hatch and feed for themselves, the single parent may have more time to feed. In chapter 6 we compare daily energy expenditure and time budgets during incubation and chick-rearing in little stint. Using dunlin as a representative of a biparental species and comparing it to the uniparental little stint, we try to answer the question what is the most energetically stressful phase and how this relates to the parental care system.

Growing up in the cold

Arctic born chicks are amongst the fastest growing shorebird chicks. Being one of the smallest of all arctic species, little stint chicks may be most vulnerable to the cold environment due to their high surface to volume ratio. We measured growth rates and energy expenditure to test the hypothesis that little stint chicks have greater energy expenditure than predicted for their body size, and that environmental variation has a strong effect on their energy expenditure and time budgets (chapter 7).

Breeding success in terms of number of chicks fledged is difficult to measure in arctic breeding shorebirds due to their cryptic behaviour and extreme camouflage. But growth rate is likely to be a good proxy for breeding success as it affects both the birds condition and the length of the period in which chicks are most vulnerable. In chapter 8 we explore how growth rates of chicks of little stint and dunlin are affected by weather and food availability.

Food peaks

The major food type for arctic chicks, and to a lesser extent for the parents as well, are surface active arthropods. They emerge once the snow has disappeared and show a strong seasonal pattern that is highly dependent on the weather. In chapter 9 we describe effects of weather and season on arthropods and use the statistical models derived from the field measurements to hindcast how the 'food for shorebird' situation must have been in the past. We discuss the effect of the timing of arthropod emergence on the timing of the shorebird breeding season and possible consequences of shifts therein due to climatic changes.

Finally I try to bring together all information in chapter 10 where I try to identify the major selection pressures acting on the timing of breeding. I conclude that the needs of parents and chicks may sometimes result in opposing selection pressures. Based on all collected information I will outline how this can be used to develop a model of the effect of arrival date and body condition on reproductive output, in terms of models of migration: the so-called 'terminal reward' function (Ens et al. 1994; Weber et al. 1998; Weber et al. 1999).

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De Arctis als vergrootglas

De meeste plekken op aarde kennen seizoenen: er is variatie in daglengte, weer en voedsel. Daarom is het voor vogels niet mogelijk om op elk moment van het jaar op elke plek te broeden, maar wordt het broedseizoen gedirigeerd door de seizoenen. Omdat de omstandigheden wat betreft weer en voedsel die nodig zijn om te kunnen broeden en kuikens groot te brengen niet geschikt zijn op de plekken waar ze de winter doorbrengen, trekken vogels in het voorjaar naar andere gebieden. Daarbij leggen ze vaak enorme afstanden af. Veel steltlopersoorten zijn zulke lange afstand-trekkers die broeden in de arctische toendra en de winter doorbrengen in gematigde of tropische streken, zoals in onze Waddenzee of op het zuidelijk halfrond (figuur 1.7).

De Arctis kenmerkt zich door extremen in weersomstandigheden. Gedurende het grootste deel van het jaar is het er slecht toeven voor de meeste organismen: bedekt met een dik pak sneeuw, temperaturen van enkele tientallen graden onder nul en aardedonker. Er zijn diersoorten die het er wel het hele jaar volhouden, doordat ze speciale aanpassingen hebben, zoals bijvoorbeeld sneeuwhoenders, sneeuwuielen, sneeuw hazen en lemmingen. Die soorten zijn in staat om voedsel te vinden onder de sneeuw en maken gebruik van de isolerende werking van het sneeuw-pak om de winter door te komen. Maar steltlopers zouden de arctische winter niet overleven. Met hun zachte snavels is het onmogelijk voedsel zoeken in de bevroren toendra. Dan zit er dus niks anders op dan weg te trekken, op zoek naar oorden waar het wel leefbaar is. Dat doen ze dan ook en aan het eind van het broedseizoen vliegen ze zuidwaarts.

De arctische zomer is kort en de tijd om een territorium te bemachtigen, een partner te zoeken, eieren te leggen, de kuikens op te voeden en de terugtocht voor te bereiden beslaat nauwelijks meer dan twee maanden. Zelfs binnen deze korte periode maakt het grillige weer het leven moeilijk. Grote temperatuurschommelingen, harde wind, regen en sneeuw buien zijn aan de orde van de dag. Daarbij komt nog dat het belangrijkste voedsel, bestaande uit insecten, een duidelijke piek laat zien: alleen in het midden van de zomer is er genoeg voedsel voor de kuikens om goed te kunnen groeien. Maar zelfs in die periode is het voedsel niet altijd beschikbaar: in reactie op het weer schommelt het aanbod van dag tot dag sterk. Daarom is het zaak om

het tijdstip van aankomst op de toendra goed te plannen. Als ze te vroeg aankomen, lopen ze het risico dat de toendra nog bedekt is met sneeuw en er niks te eten is. Na een lange vlucht hebben ze niet veel energie over om zonder voedsel te overleven en bovendien hebben ze extra voedsel nodig om een territorium te veroveren en eieren te kunnen leggen. Maar als ze te laat aankomen en beginnen met broeden, worden hun kuikens te laat geboren en missen ze de voedselpiek.

Dit betekent overigens niet dat het belang van een goed getimed broedseizoen alleen beperkt is tot de Arctis of dat de tijdsdruk hier per se sterker is dan in meer gematigde streken. Zo'n krappe voedselpiek komt namelijk op meer plekken voor. Maar in de Arctis is niet alleen de temperatuur lager, waardoor de vogels meer energie nodig hebben, ook de grilligheid van het weer maakt dat de energetische grenzen zich duidelijker aftekenen. Hierdoor is het waarschijnlijk dat de effecten van timing op de voortplanting in de Arctis duidelijker zichtbaar en makkelijker te ontdekken zijn dan in gematigde gebieden. Als door een vergrootglas worden de processen die te maken hebben met de timing uitvergroot. Bovendien hebben de poolgebieden, zowel de Noord- als de Zuidpool in het verleden de sterkste klimaatveranderingen laten zien en is de voorspelling dat ook in de toekomst de effecten van klimaatveranderingen hier het sterkst en het eerst merkbaar zullen zijn. Zoals Al Gore in zijn film 'An Inconvenient Truth' aangaf: de polen zijn de spreekwoordelijke 'kanaries in de kolenmijn'.

De vraag waarom steltlopers überhaupt zulke enorme afstanden afleggen om in de Arctis te kunnen broeden is natuurlijk mateloos interessant, maar komt in dit proefschrift slechts zijdelings ter sprake. De centrale vraag waar alle deelvragen die in dit proefschrift aan de orde komen om draaien is: wat zijn de beperkingen waar steltlopers mee te maken krijgen doordat ze broeden in de Arctis, waar het broedseizoen kort is en de weersomstandigheden uiterst grillig zijn. En hoe belangrijk is een goede timing hierbij?

Het onderzoek dat ten grondslag ligt aan dit proefschrift hebben we uitgevoerd in 2000-2002 in Medusa Bay op het Taimyr schiereiland in centraal Siberië (figuur 1.5). De belangrijkste soorten waar we in ons broedgebied mee te maken hebben zijn kleine strandloper, krombekstrandloper, bonte strandloper, steenloper, kleine

goudplevier en bontbekplevier. Hiervan spelen de eerste drie de meest prominente rol in dit proefschrift.

De volgorde van de verschillende hoofdstukken volgt grofweg het seizoen:

na de aankomst op de toendra in de eerste helft van juni (hoofdstuk 2) worden de nesten gemaakt en de eieren gelegd (hoofdstuk 3) en begint een periode van zo'n drie weken broeden (hoofdstukken 3, 4, 5, 6). Vanaf begin juli worden de kuikens geboren en groeien in ca twee weken op (hoofdstukken 6, 7, 8). Door het hele seizoen is de voedselbeschikbaarheid (hoofdstuk 9) van groot belang. Om het geheel wat beter leesbaar te maken voor niet-vakgenoten wordt elk hoofdstuk vergezeld van een kort (en hopelijk voor iedereen begrijpelijk) stukje in het Nederlands.



Chapter 2



Ingrid Tulp
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Body condition of shorebirds upon arrival at their Siberian breeding grounds

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Shorebirds that breed in arctic areas migrate long distances from their wintering grounds. To fulfil these journeys they carry substantial stores, which are gradually depleted during the migratory flight. The remains of these stores could potentially be used for egg formation, insurance against poor food conditions upon arrival in the breeding area or for rebuilding organs that were reduced prior to migration. We quantified body condition in seven shorebird species caught upon arrival in Taimyr, Siberian Arctic. In addition to body mass we measured total body water (TBW) using the deuterium dilution method in a subset of birds caught to estimate lean body mass and fat mass. We also caught shorebirds during incubation and in dunlin and little stint TBW measurements were carried out for incubating individuals. To investigate possible functions of arrival stores, arrival condition is compared with condition during incubation.

Arrival body mass was highly variable and was significantly lower than mass during incubation in all species (after correction for structural size), but 3-18% above the mean mass of these species in their African winter quarters. Fat index varied between 6.6% and 14.6 %. Fat stores were estimated to secure survival for 0.8 days in the smallest to 2.8 days in the largest species. The increase in mass from the arrival to the incubation period was not caused by post-arrival accumulation of fat, but by an increase in lean mass, as quantified in little stint and dunlin.

Introduction

Arctic breeding birds generally undertake long migrations from their wintering areas to the breeding grounds. The arctic summer is short and time available for finding a mate, laying eggs, raising chicks and preparing for return migration comprises hardly more than two months. Within this short period, food availability usually shows a short seasonal peak, particularly for birds that feed on invertebrates living on the tundra surface (MacLean and Pitelka 1971; chapter 9). An optimal use of the short breeding season is therefore essential for successful reproduction.

For many arctic breeding birds, an early arrival on the tundra in a condition that allows a quick start of breeding may maximise the chances of reproductive success. However, for arctic birds there is also a risk to early arrival: the tundra may still be snow-covered and frozen and offer no food to arriving birds.

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

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

A third possible function of arrival stores is that these are used to rebuild organs that were reduced for the migratory flight but are needed during (preparation for) the reproductive phase. Red knots and ruddy turnstones *Arenaria interpres* were shown to arrive at Ellesmere Island (Canada) with relatively large fat and muscle stores (Morrison and Davidson 1990; Morrison et al. 2005). During the post arrival period these declined in size and the digestive system, heart and liver increased.

Hence, even if eggs are formed from locally assembled nutrients, the energy stores that arctic shorebirds carry upon arrival on their breeding grounds can still be functional for reproduction. Due to the logistic difficulties of capturing birds directly upon arrival, few empirical data are available on dynamics of body mass and nutrient stores in this period. Existing studies have been carried out in Nearctic areas only (Morrison and Davidson 1990; Farmer and Wiens 1999; Morrison et al. 2005; Krapu et al. 2006).

In view of the dynamics of organ size during premigratory fattening, migration and post-arrival (Piersma and Gill 1998; Piersma et al. 1999; Battley et al. 2000), it is useful not only to have insight in total arrival mass, but also in the relative proportion of fat stores and lean tissue. In this paper we describe variation in the arrival condition of several palearctic shorebird species on the breeding grounds in the tundra of the Taimyr Peninsula, Siberia, Russia. Total body mass was measured in all species. In a selection of species lean (fat-free) mass and fat mass were estimated with the deuterium dilution method (Speakman et al. 2001). We compare body condition (total body mass, lean mass, fat stores) at arrival with data for the same species at other times of the year, and explore the potential value of the energy stores in terms of reduced starvation risk.

Study site

Data were collected between June and mid August of 2000, 2001 and 2002 at Medusa Bay, 18 km south of Dikson on the west coast of the Taimyr peninsula, Siberia, Russia (73°20'N 80°30'E). The habitat can be characterised as arctic tundra (Chernov 1985). Vegetation consists of moss, lichen, grass, sedges and dwarf willows generally not higher than 30 cm with a significant proportion of the surface bare ground. The landscape has a rolling relief with scattered stony ridges. For a more detailed description we refer to Schekkerman et al. (2004). Snow melt in the study area usually started on 5-12 June, egg-laying of shorebirds mostly took place between 15 June and 10 July. Shorebird species that pass through but also breed at the site include dotterel *Charadrius morinellus*, little stint *Calidris minuta*, dunlin *C. alpina*, curlew sandpiper *C. ferruginea*, pectoral sandpiper *C. melanotos*, red phalarope *Phalaropus fulicarius* and ruddy turnstone. Species that pass by to breed up to several hundreds of kilometres further north and east on the peninsula include red knot, sanderling *C. alba*, and purple sandpiper *C. maritima*.

Methods

Catching arriving birds

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

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

Table 2.1. Mean body mass of all shorebirds caught at Medusa Bay in 2000-2002 (with standard deviation, range and sample size). Means are given for age and sex classes separately, and for the arrival and incubation phase. Recaptured birds are included only once (first capture) within each phase.

species	sex	arrival					incubation				
		mean	SD	min	max	N	mean	SD	min	max	N
dotterel	all	124.5	7.2	112.0	140.0	26	110.5	0.7	110.0	111.0	2
red knot	all	130.1	8.1	120.0	138.5	5					
sanderling	male	48.5	4.9	45.0	52.0	2					
little stint	all	26.0	3.6	20.5	36.2	22	29.1	2.6	23.7	37.3	235
curlew sandpiper	all	58.4	4.0	51.0	68.5	36	64.7	4.2	56.5	72.3	28
	female	60.4	4.5	53.0	68.5	16	64.7	4.2	56.5	72.3	28
dunlin	male	56.8	2.7	51.0	60.5	20					
	all	48.9	3.9	41.8	57.1	28	53.3	3.5	45.5	62.0	81
	female	51.9	3.4	45.3	57.1	9	54.9	3.3	48.2	62.0	37
purple sandpiper	male	47.4	3.3	41.8	54.5	19	51.9	3.2	45.5	60.5	42
	all	69.3	0.1	69.2	69.3	2					
red phalarope	all	58.3	8.0	46.3	71.0	16	50.9	6.2	40.0	59.0	7
	female	61.1	6.9	50.5	71.0	12					
	male	49.8	4.1	46.3	54.7	4	50.9	6.2	40.0	59.0	7
ruddy turnstone	all	102.5	8.3	94.0	123.0	15	101.4	5.7	97.7	108.0	3
	female	108.9	9.9	95.0	123.0	6	108.0		108.0	108.0	1
	male	98.3	2.9	94.0	103.0	9	98.1	0.6	97.7	98.5	2

Catching birds during incubation

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

Biometric measurements

Captured birds were ringed with metal rings and measured. Bill length was measured to the nearest 0.1 mm using callipers. Wing length (maximum chord, 1 mm) was measured with a stopped ruler. Spring balances were used to measure body mass (to 0.1 g). All birds were weighed within 10 minutes after capture. Dunlins, curlew sandpipers, ruddy turnstones and red phalaropes were sexed based on plumage characteristics and size. Red knot, little stint and dotterel could not be reliably sexed on external characters.

Deuterium measurements

Measurements of Total Body Water (TBW) were used to separate total body mass into fat mass and lean mass. TBW was measured using the deuterium dilution method (Lifson and McClintock 1966; Speakman 1997; Visser et al. 2000; Speakman et al. 2001) in a subset of the curlew sandpiper, dotterel, dunlin, red knot, little stint, sanderling and ruddy turnstone

Table 2.2. Results of TBW measurements.

Sample size, mean total body mass, TBW, lean mass, fat mass (plus standard deviation and range) and fat index (% of lean mass) are given per species and phase.

species	phase	n birds	total body mass (g)			TBW(%)			lean mass			fat mass (g)			fat index				
			mean	SD	min	max	mean	SD	min	max	mean	SD	min	max	min	max			
dotterel	arrival	8	121.4	7.4	112.0	130.0	65.4	1.5	63.4	67.2	113.4	7.9	103.8	122.5	8.0	2.6	5.0	12.3	7.0
	arrival	3	126.0	7.9	120.0	135.0	61.2	4.4	56.7	65.4	109.9	4.7	105.5	114.9	16.1	8.9	8.1	25.7	14.6
little stint	arrival	16	25.3	2.5	21.9	31.3	65.8	4.0	56.1	70.1	23.7	2.4	20.3	30.6	1.6	1.6	0.0	5.2	6.6
	incubation	11	28.7	1.8	25.7	32.0	66.2	4.7	57.5	72.2	27.0	1.7	24.0	29.9	1.6	2.1	-0.9	5.5	6.0
curlew sandpiper	arrival	24	59.0	4.5	51.0	68.5	63.7	2.7	57.9	70.3	53.6	3.6	48.0	61.1	5.4	2.5	-0.2	11.5	10.1
	arrival	4	48.4	3.4	45.0	53.0	63.8	3.8	61.5	69.4	44.0	2.1	42.2	46.6	4.4	2.7	0.4	6.4	10.0
dunlin	incubation	9	52.2	4.7	44.3	59.2	66.8	3.7	59.9	71.1	49.7	3.4	44.9	55.4	2.5	3.0	-0.7	7.9	5.1
	arrival	2	48.5	4.9	45.0	51.9	64.0	0.3	63.8	64.2	44.3	4.2	41.3	47.3	4.2	0.6	3.7	4.6	9.4
sanderling	arrival	8	102.9	9.4	95.0	123.0	62.2	3.3	57.5	67.3	91.2	7.0	83.4	105.9	11.7	5.4	3.6	19.5	12.8
turnstone	arrival	8	102.9	9.4	95.0	123.0	62.2	3.3	57.5	67.3	91.2	7.0	83.4	105.9	11.7	5.4	3.6	19.5	12.8

that were caught upon arrival (see tables 2.1 and 2.2 for sample sizes). In addition to experiments carried out in this study, TBW measurements of incubating little stints and dunlin collected in 2000-2002 that were published elsewhere (chapter 6) are also used.

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

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

These values were corrected for the slight but systematic overestimation of the deuterium dilution method relative to other methods for the assessment of the amount of body water (Speakman et al. 2001). Assuming that lean mass contains 70% water (Speakman et al. 2001), lean (fat-free) body mass can be calculated as:

$$\text{lean mass (g)} = TBW \text{ (g)} / 0.7$$

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

Analyses

For each species, we calculated mean total body mass for all birds caught upon arrival in the area, and compared this with masses measured during the incubation phase, and with published values from the species' African wintering areas (red knot 119 g, sanderling 47 g, little stint 22 g, curlew sandpiper 52 g, (Zwarts et al. 1990); ruddy turnstone 99 g, (Ens et al. 1990); dunlin: 47 g, (Van der Have 1997) dotterel: 110 g, (Cramp and Simmons 1983)).

Second, we estimated lean mass and fat stores for the subset of birds in which TBW measurements were made, and compared these between phases of reproduction and between sexes. To expand our findings to a larger dataset, we then used the relationship between lean mass and structural size derived from this subset of birds to estimate lean mass and fat stores for all other trapped birds for which TBW information was lacking. On the basis of this extended dataset we again analysed patterns in fat stores and lean mass. Because individual variation in mass and body composition was also of interest, species means are given ± SD unless stated otherwise.

Arrival body mass was compared with body mass during incubation after correcting for possible effects of structural size, using multiple linear regression. The best fitting

structural measurement (wing, bill or total head length) was used to correct for structural size, after which effects of sex or phase (arrival vs. incubation) were tested. Due to a small sample size for some species in the incubation phase, comparisons were only carried out for little stint, dunlin and curlew sandpiper (best fitting structural measurement for little stint: wing length, dunlin: bill length and curlew sandpiper: total head length).

In species in which at least four TBW measurements per phase/sex were made (dunlin, little stint and curlew sandpiper) we carried out regressions to compare lean mass between periods or sexes, again after correcting for the effect of structural size. The species-specific regressions of lean mass on structural size were then used to estimate lean mass and fat mass of those birds in which no TBW measurements were carried out. The effect of phase (arrival vs. incubation) was included in the regressions for dunlin and little stint. For curlew sandpiper this was not possible, since no TBW measurements were made during the incubation phase, and the regression was used to predict the lean mass and fat mass of birds in the

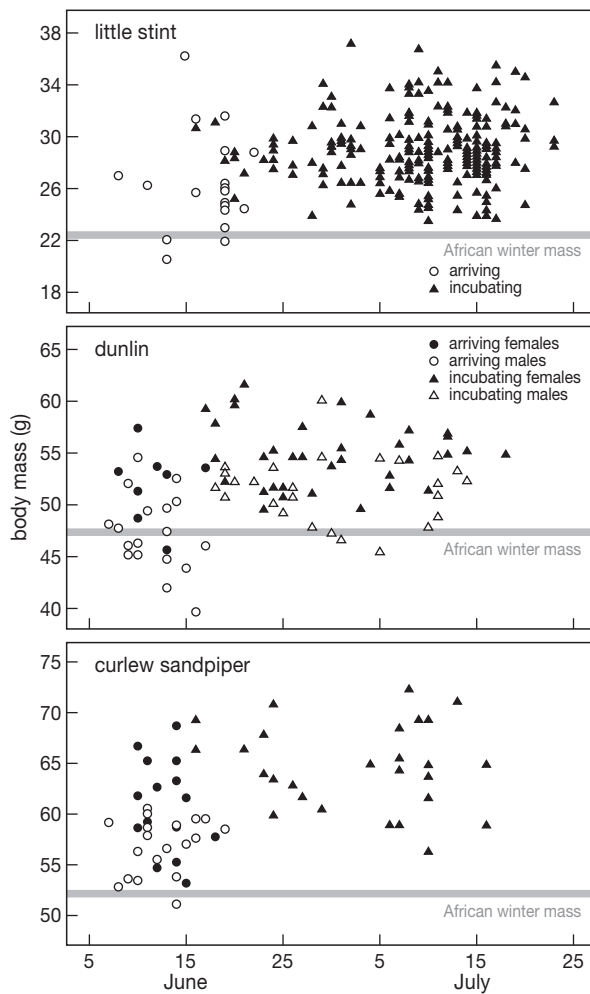


Figure 2.1. Body mass for little stint, dunlin and curlew sandpiper in relation to catching date for birds caught during arrival and incubation. For comparison the values for African winter mass are also indicated (Zwarts et al. 1990; Van der Have 1997).

arrival period only. Using this extended dataset of reconstructed fat and lean mass we again tested for differences between phases and sexes in fat mass. As structural size and phase were used as predictors of lean mass, and structural size is also correlated with sex, it was not possible to perform any tests on reconstructed lean mass (such test would result in a saturated model). Thus, in this paper we use two measures of fat mass and lean mass: fat mass based on measured lean mass (deuterium dilution method “TBW based fat/lean mass”) and fat mass based on lean mass estimated from structural size (“reconstructed fat/lean mass”).

Results

Arrival mass

In seven species for which published total body mass values are available from their African wintering grounds, mean arrival mass in Taimyr was on average 9.0% (SD 5.9%, $N = 7$) above mean winter mass in Africa. This difference was smallest in ruddy turnstone (3.1%) and largest in little stint (17.6%).

In most species arrival body mass was highly variable between individuals (figure 2.1, figure 2.2, table 2.1). Little stint and red phalarope showed the largest variation in body mass between individuals (CV = 10.0% and 13.8% respectively), while dotterel, dunlin, curlew sandpiper and ruddy turnstone showed less variation (CV = 5.8, 6.6, 6.5 and 5.7% respectively).

Body mass in arriving versus incubating birds

After correction for wing length, newly arriving little stints weighed significantly less than incubating individuals (wing length $F_{1,227} = 25.14$, $P < 0.001$, phase: $F_{1,227} = 34.59$, $P < 0.001$, figure 2.1). In dunlin females were significantly heavier than males and both sexes weighed less upon arrival than during incubation (bill: $F_{1,103} = 33.03$, $P < 0.001$, sex: $F_{1,103} = 5.73$, $P = 0.019$, phase: $F_{1,103} = 34.19$, $P < 0.001$, figure 2.1). Restricting the analysis to arriving birds only, the difference between the sexes was not significant after correction for bill length (bill: $F_{1,26} = 13.25$, $P = 0.001$, sex: $F_{1,26} = 0.55$, $P = 0.467$).

As curlew sandpiper males do not incubate and were therefore only caught in the arrival period, we restricted the comparison between phases to females. Incubating females were significantly heavier than females that had just arrived (total head: $F_{1,42} = 1.16$, $P = 0.287$; phase: $F_{1,42} = 182.83$, $P = 0.003$, figure 2.1). Among arriving birds, females were significantly heavier than males ($F_{1,32} = 8.99$, $P = 0.005$) while total head did not improve the model ($F_{1,32} = 2.94$, $P = 0.096$). Also in this case the effects of total head and sex on body mass were interchangeable.

Dotterel caught in the arrival period were all heavier than the two incubating males caught later in the season (not tested, figure 2.2). In red phalarope there was no difference in arrival mass between sexes after correction for structural size (wing: $F_{1,13} = 8.79$, $P = 0.011$, sex: $F_{1,13} = 0.57$, $P = 0.462$). In males (the incubating sex), mass at arrival did not differ from that of incubating birds (wing: $F_{1,8} = 3.67$, $P = 0.092$, phase: $F_{1,8} = 0.18$, $P = 0.682$, figure 2.2). Within the arrival period female turnstones weighed significantly more than males (wing $F_{1,13} = 0.59$, $P = 0.456$, sex $F_{1,13} = 9.43$, $P = 0.009$). Insufficient weights were taken in the incubation period for a formal comparison, but these were similar to the masses observed at arrival (figure 2.2).

TBW-based lean mass and fat store

The average lean mass at arrival in Taimyr as determined by the isotope dilution method in seven species (table 2.2) was on average 0.6% (SD 6.1%, $N = 7$) below the mean winter

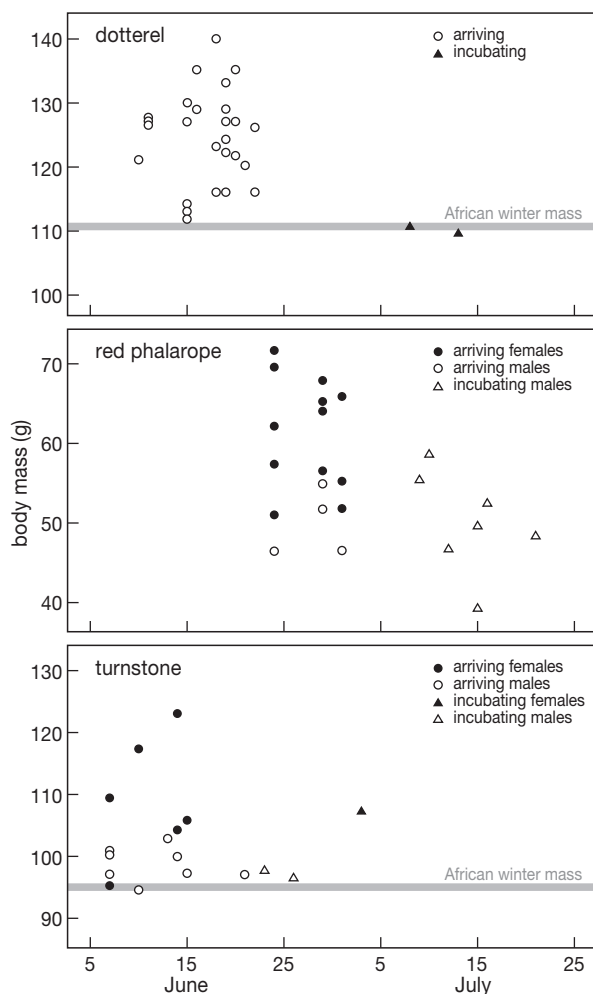
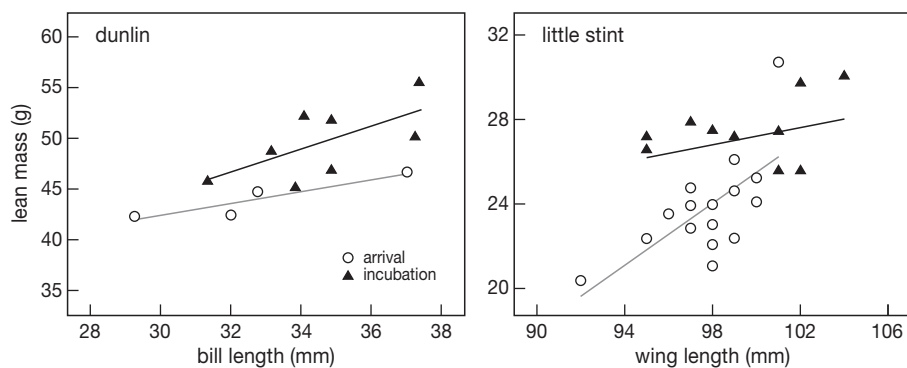


Figure 2.2. Body mass for dotterel, red phalarope and turnstone in relation to catching date for birds caught during arrival and incubation. Because of low sample sizes no statistics were carried out for these species. For comparison the values for African winter mass are also indicated (Cramp and Simmons 1983; Ens et al. 1990). For red phalarope no winter mass values are available.

Figure 2.3. Lean mass in relation to structural size for dunlin and little stint in the arrival versus the incubation phase.



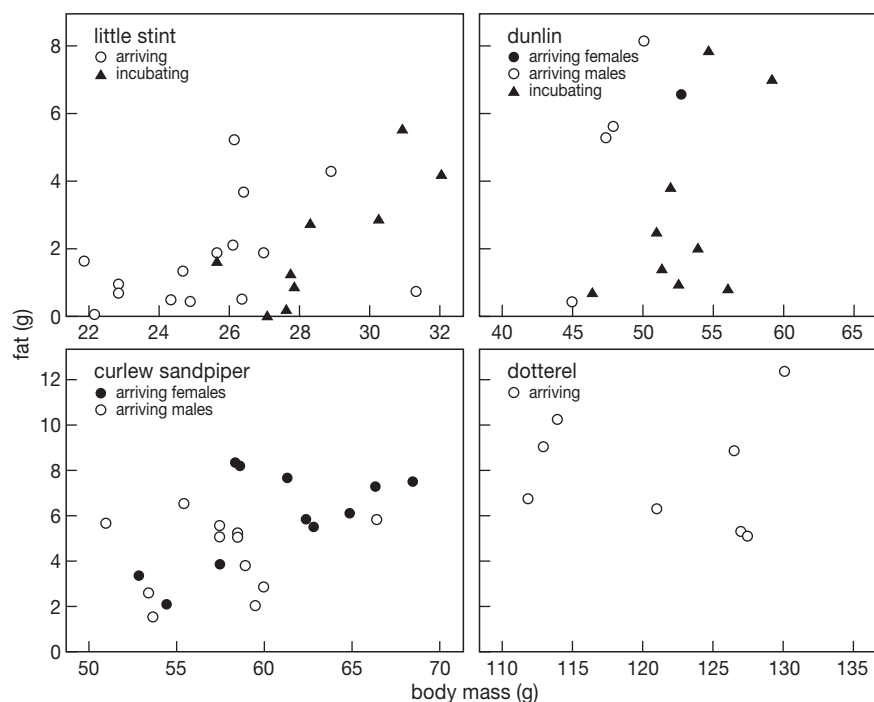
mass of the same species in Africa. Compared to this yardstick, lean mass upon arrival was lowest in red knot (-8.0%) and highest in little stint (+7.2%). In dunlin and little stint lean mass was measured in both arriving and incubating birds (table 2.2). After correction for structural size, lean mass was significantly larger during incubation than upon arrival in both species (table 2.3, figure 2.3). After correction for structural size, there was no difference between the lean mass of arriving female and male curlew sandpipers (total head length: $F_{1,22} = 14.68$, $P = 0.001$, sex $F_{1,22} = 0.52$, $P = 0.480$). In dunlin the sample size of arriving birds was too small to test for a sex effect.

Expressing fat stores as an index (fat mass / lean mass) gives the possibility to compare fat stores across species and phases (table 2.2). For the seven species, the mean fat index upon arrival was on average 9.9% (SD = 2.5%, $N = 7$, table 2.2). It varied between species from 6.8% in little stint to 14.2% in dotterel, and was not significantly related to the species' lean mass ($F_{1,5} = 1.75$, $P = 0.24$). Fat stores did not differ significantly between arriving and incubating little stints (wing: $F_{1,25} = 0.16$, $P = 0.691$, phase: $F_{1,25} = 0.01$, $P = 0.938$, figure 2.4). Fat stores of dunlin did not differ between the arrival and incubation phases nor between the sexes (bill: $F_{1,11} = 0.05$, $P = 0.832$, sex: $F_{1,11} = 1.37$, $P = 0.266$, phase: $F_{1,25} = 1.16$, $P = 0.305$). Arrival fat stores in curlew sandpiper did not differ significantly between the sexes (total head: $F_{1,22} = 0.07$, $P = 0.795$, sex: $F_{1,22} = 0.00$, $P = 0.994$).

Table 2.3. Regressions of lean mass estimated from TBW measurements on structural size, used to estimate fat stores of birds of which no TBW measurements were taken. For little stint and dunlin a distinction was made between arriving and incubating birds (see figure 2.3), for curlew sandpiper only data for arriving birds were available. In curlew sandpiper and dunlin the effect of sex was not significant, in little stint it could not be tested. The interaction between size and phase was not significant in dunlin.

species	parameter	estimate	SE	F	P	R ²
little stint	constant	17.9	16.4			53.5
	wing length	0.093	0.166	8.71	0.007	
	phase			18.88	<.001	
	arrival	-65.0	26.7			
	incubation	0	0			
	wing length.phase			5.36	0.030	
	arrival	0.631	0.273			
	incubation	0	0			
curlew sandpiper	constant	10.7	11.7			30.3
	total head length	0.69	0.187		<0.001	
dunlin	constant	19.9	11.4			61.0
	bill length	0.86	0.33	14.38	0.004	
	phase			6.36	0.03	
	arrival	-4.13	1.64			
	incubation	0	0			

Figure 2.4. Fat mass as estimated from TBW measurements in relation to total body mass for little stint, dunlin, curlew sandpiper and dotterel.



Reconstructed fat stores

Overall, the reconstructed lean mass resembled closely the mean measured lean masses in the same species and phase of the breeding cycle (average difference 0.7% of measured value, SD = 1.3, range -0.1-2.7 %, N = 5, table 2.2, table 2.4). In little stint and dunlin reconstructed fat mass at arrival was not significantly different from that during incubation (table 2.4). Upon arrival there were no significant differences in fat store between the sexes, neither in dunlin nor in curlew sandpiper. Reconstructed fat index varied between species from 7.5% in incubating little stint to 9.2% in arriving curlew sandpiper (table 2.4).

Discussion

What is 'arrival mass'?

Our observations add significantly to the existing volume of data on body condition of shorebirds arriving on their arctic breeding grounds. Migratory body and organ mass dynamics have been particularly well-studied in this group of birds, but the remoteness of and difficult conditions on their breeding grounds, as well as the difficulty of catching adequate samples of birds while they spread out across the vast tundra, have led to few data being available from this important stage of the annual cycle.

Our catching method using clap net and tape lures appeared to be successful in trapping recently arrived shorebirds and birds completing the last part of their migratory flight. The appearance of certain species, such as curlew sandpiper and little stint, within the study area was quite abrupt in time, and most of our catches closely followed this moment of arrival. Once birds started to display territorial and courtship behaviour, they were less easily attracted to the nets. An exception to this was Eurasian dotterel, which appeared to fly around in the area looking for a mate and were strongly attracted to the play-backed sound of displaying conspecifics.

A significant proportion of the trapped birds were observed descending from high altitudes in response to the playback sounds, or were trapped in flight when they were cruising low above the ground into northeasterly winds. It is therefore likely that our sample not only consisted of birds that had the intention to stop at our study site, regardless of the attraction of the play-backed sounds, but also of birds that would have moved on had they not been attracted by the sounds. Therefore we can not be certain that all of the birds caught had reached their final destination. Species like curlew sandpiper, little stint, dunlin and ruddy turnstone all breed in the study area but have a wide breeding distribution and may have moved on after capture. Of species that do not or only rarely breed in the area, like sanderling, red knot and dotterel, we are certain that they had not reached their breeding area yet. However, all these birds must have been on the final leg of their migration, with their final breeding destination 0 to 1000 km away (northeastern tip of the Taimyr Peninsula). This would mean that the average distance yet to be covered is c. 10% of the total (great circle) distance between ultimate spring stopover sites in north-west Europe and southwest Siberia (c. 4800 km, Henningsson and Alerstam 2005).

For this group of birds, there is the possibility that the trapping method resulted in a non-random selection of birds. Individuals with depleted reserves might be more prone to interrupt their flight in response to the tape lures than birds that still have enough reserves left to continue their journey northward. While we cannot exclude this possibility, we note that individuals that descended from high altitudes showed a considerable variation in body masses.

Table 2.4. Reconstructed lean mass and fat stores (in g and as fat index = % of lean mass) in the arrival period and for little stint and dunlin also during incubation. N denotes the number of birds in which TBW measurements were made (table 2.2) + the number for which lean mass and fat mass were predicted from a regression of TBW lean mass on structural size. These numbers can deviate from the numbers in table 2.1, because for some individuals not all required structural size measurements were taken.

species	N	phase	reconstructed lean mass				reconstructed fat mass				reconstructed fat index			
			mean	SD	min	max	mean	SD	min	max	mean	SD	min	max
little stint	16+6	arrival	24.0	1.7	19.5	27.5	2.0	3.5	-7.0	10.2	8.5	13.8	-25.4	39.1
	11+220	incubation	27.0	0.9	17.9	27.7	2.0	2.5	-3.1	10.6	7.5	9.2	-11.3	39.5
curlew sandpiper	24+11	arrival	53.5	1.8	50.9	58.2	4.9	3.5	-0.9	14.3	9.2	6.5	-1.6	26.5
dunlin	4+24	arrival	45.1	2.5	41.0	51.0	3.7	3.2	-1.9	10.7	8.3	7.2	-4.1	25.9
	9+57	incubation	49.6	2.2	45.5	54.8	4.1	3.1	-3.0	10.9	8.4	6.3	-6.2	22.1

We also cannot exclude that shorebirds for which Medusa Bay was their final destination, had already stopped for a few days in snow-free tundra patches further south. Two observations suggest that this may have happened. The arctic spring of 2002 was delayed with snow cover dropping below 50% nine days later than in 2000-2001. In the first half of June 2002 we counted numbers of staging shorebirds in our study area that exceeded the number later found breeding in several species, and that disappeared as soon as warmer weather initiated snow melt (Schekkerman et al. 2004). Ring-reading showed that this early wave in dunlin consisted of non-local birds, as 50% of the site-faithful local birds had been individually colour-marked in the previous years. Colour-marked dunlin arrived on average six days later in 2002 than 2001, and started laying seven days later (Schekkerman et al. 2004). These observations suggest that shorebirds arriving in Taimyr do not fly directly to their previous year's breeding site but adjust their progress across the tundra to local snow conditions by making one or more stops short of their final destination. Therefore 'arrival' in continental tundra areas like Taimyr should perhaps not be considered a discrete process, in the way that it may be in areas where shorebirds arrive after a long-distance flight across a large ecological barrier with few or no options for short-stopping, like Greenland and the northeastern Canadian Arctic.

General patterns in arrival condition

The average fat index (fat mass / lean mass) of waders arriving in Taimyr varied between species from 7% to 15%. Because premigratory accumulation and migratory depletion of nutrient stores are known to involve not only fat but also proteins in muscles and multiple other body organs (Piersma and Gill 1998; Piersma et al. 1999; Battley et al. 2000), lean mass does not provide a constant yardstick for comparing stores between individuals or between different phases of the annual cycle. Therefore we compared our observations with the mean mass of the studied species in their African winter quarters, representing a part of the annual cycle where no premigratory fattening takes place and when birds need to carry few energy stores as an insurance against periods of hardship. The body mass of shorebirds wintering in W-Africa comprises about 3-8% fat on average (Zwarts et al. 1990).

Average body mass of waders arriving in Taimyr was 3-18% (mean 9%) above the African winter mass of these same species. Average lean mass at arrival was between 8% below and 7% above mean African winter mass (mean 1% below), and thus on average slightly (c. 5%) above the lean mass of wintering birds. On average therefore, the birds arrived in Taimyr with some energy stores remaining, but generally not a large amount. However, these averages hide a large variation between individuals (figures 2.1 and 2.2). This variation may arise from differences in body condition at departure from the last staging area, in conditions encountered during the migratory flight, or in the time that birds had been already present in the Arctic and the conditions encountered there.

Studies in the Nearctic also describe fat stores upon arrival. Morrison (2006), who caught and collected red knots upon arrival and in the post-arrival phase at Alert, Canada, found that the earliest arriving birds carried substantial stores of fat and protein, but that these were lost rapidly after arrival. Arriving red knots still carried on average 42 g fat, which is much higher than the 16 g observed in our study. This difference could suggest that only relatively lean red knots came down at our study site, or it could be a genuine reflection of differences in mass between birds arriving after a flight across the ocean and/or the Greenland ice cap, and birds arriving after a flight across the northern Eurasian coastline where opportunities for stopping short of the final destination may be encoun-

tered. Semipalmated sandpipers *Calidris pusilla* and white-rumped sandpipers *Calidris fuscicollis* arrived in the southernmost part of their breeding ranges near Churchill, Manitoba, with average fat indices of 12.5% and 13.5% (calculated from Krapu et al. 2006). These species depart North Dakota with fat indices of 22.0% for semipalmated sandpiper and 24.5% for white-rumped sandpiper. Little stints are similar in size to semipalmated sandpipers, but arrived with a lower mean fat index (6.6%). Sanderling and dunlin are similar in size to white-rumped sandpiper and also arrive with lower fat indices (9.4 and 10.0 %). These differences (at least for dunlin) might be due to the fact that these American species were caught at the very southern part (or for white-rumped sandpiper, even 400 km south) of the breeding range.

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

A possible function of arrival stores could be insurance in case upon arrival feeding is not yet possible due to snow cover. The average fat stores with which the birds arrive varied between 1.6 for little stint and 16.1 g for red knot (table 2.2). Assuming a daily energy expenditure (DEE) of 2.3 times basal metabolic rate (BMR, Wiersma and Piersma 1994), using published BMR values (Lindström and Klaassen 2003) and an energetic equivalent of 39 kJ per g fat, these fat stores can secure survival for 0.8 (little stint) to 2.8 days (red knot) if the bird is forced to fast (table 2.5). Survival times are positively related to arrival body mass among species ($F_{1,6} = 11.99$, $P = 0.017$). The maximum fat stores measured enable a survival period of 1.7 days in sanderling (minimum) to 4.4 days in red knot (maximum, table 2.5). In addition to fat stores, also part of the protein reserves in the body (lean mass) are metabolised before birds starve to death. Because of the lower energy content of protein, these reserves will contribute less to survival time than fat stores. Although not much, these stores could provide some leeway if conditions upon arrival prevent feeding (because of snow cover), or at least give time to look for nearby sites where spring is more advanced.

Table 2.5. Estimated survival times based on arrival fat stores (table 2.2, published BMR values (Lindström and Klaassen 2003), the assumption of a DEE of 2.3 BMR (Wiersma and Piersma 1994) and an energetic equivalent of 39 kJ/g fat.

species	body mass (g)		fat mass (g)		BMR (W)	[2.3 BMR]	DEE (kJ)	survival (N days)	
	mean	mean	min	max			mean	min	max
dotterel	121.4	8.0	5.0	12.3	1.1	221.9	1.4	0.9	2.2
red knot	126.0	16.1	8.1	25.7	1.1	227.9	2.8	1.4	4.4
little stint	25.3	1.6	0.0	5.2	0.4	73.5	0.8	0.0	2.8
curlew sandpiper	59.0	5.4	-0.2	11.5	0.6	121.2	1.7	0.0	3.7
dunlin	48.4	4.4	0.4	6.4	0.6	119.2	1.4	0.1	2.1
sanderling	48.5	4.2	3.7	4.6	0.5	105.3	1.5	1.4	1.7
turnstone	102.9	11.7	3.6	19.5	0.9	186.8	2.4	0.8	4.1

Function of nutrient stores upon arrival: rebuilding organs?

In the prebreeding phase shorebirds need to acquire not only reserves necessary for egg formation but also the future parents must remain in good condition to make it through the time- and energy demanding incubation period. Especially small sized shorebirds and specifically the species that perform incubation duties alone (little stint and curlew sandpiper) need excess reserves to overcome bad weather periods during breeding (chapters 4 & 5). Arrival with some stores remaining can give them a head start. Morrison (2006) concluded that in red knots metabolites that become available from arrival stores are used to enable body changes, such as an increase in organs related to the digestive system. For most species in our study, arrival body mass was lower than that during incubation (table 2.1). For those species of which fat stores were measured both during arrival and incubation (dunlin and little stint), fat indices were higher in arriving than in incubating birds; this was not due to lower fat mass but to an increase in lean mass during incubation. This finding supports the idea that nutrient stores upon arrival may be used to rebuild organs, but as total body mass increased it is also clear that exogenous nutrients, collected after arrival on the breeding grounds, must make a large contribution to this.

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

Stores carried to the tundra may provide nutritional resources that are necessary for egg formation and can not be collected there. If arrival stores play a role in egg formation, differences between sexes in arrival stores are expected (Smith and Moore 2003). In dunlin, curlew sandpiper and ruddy turnstones, females were significantly heavier in the arrival period, but body mass did not differ between the sexes in red phalarope (although sample size for males was very low). However, these sex differences could not be distinguished from a size effect (structural size measures were interchangeable with sex in the analyses). For curlew sandpiper, the only species for which enough TBW measurements were carried out on both sexes in the arrival period, we did not find a significant difference in either fat stores or lean mass in the arrival period after correction for structural size. The larger dataset of reconstructed fat stores showed no sex differences in fat stores upon arrival in dunlin or in curlew sandpipers. Also in red knots Morrison (2006) did not record



differences in fat store between the sexes. The 'reconstructed' lean masses could not reveal a difference between the sexes, as lean mass was predicted on the basis of the TBW dataset, and no sex effect was found there.

Based on our data we can not rule out that females bring specific nutrients to the breeding area, necessary for egg formation or organ build-up, that do not show up in a difference in mass of body stores. Morrison and Hobson (2004) and Klaassen et al. (2001) however, have shown that eggs of red knots and other shorebird species consist of local terrestrial nutrients and only the earliest laid eggs showed some possible input of nutrients from marine resources originating from wintering sites. Stores still present upon arrival are therefore likely not to be used for egg production but for rebuilding organs and as an insurance against bad food conditions upon arrival.

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De aankomst op de toendra

Steltlopers die op de Siberische toendra broeden komen van ver. Vaak hebben ze een reis van ettelijke duizenden kilometers achter de rug. Volgevreten zijn ze vertrokken uit gebieden zoals bijvoorbeeld de Waddenzee en in een periode van enkele weken vliegen ze met hooguit een enkele tussenstop voor een snelle hap naar het noorden. Want ze hebben haast. De zomer in het hoge noorden duurt niet lang en het weer is er grillig, dus is het zaak om zo vroeg mogelijk aan te komen. Liefst vroeger dan soortgenoten, want dan is het makkelijker om een goed territorium te veroveren. Maar ook weer niet te vroeg, dan is de kans groot dat er nog zoveel sneeuw ligt dat er niks te eten is. Wanneer de vogels vertrekken zijn ze helemaal uitgebalanceerd en afgetraind: voldoende brandstof in de vorm van vet en eiwitten om de vliegspieren van energie te voorzien en organen die ze onderweg niet nodig hebben zijn ingekrompen om het gewicht te beperken. Als volleeerde barbapappa's zijn ze omgevormd van calorieënstouwers tot superzuinige aerodynamische vliegers. Doordat ze relatief klein zijn en zuinig moeten vliegen is er weinig extra ruimte om een voorraad mee te nemen voor na de vlucht, bij aankomst op de toendra. Dat is anders bij grotere vogels, zoals ganzen en zwanen, die bij aankomst nog genoeg voorraad hebben om snel eieren te kunnen leggen. Als steltlopers in staat zouden zijn ook iets van die reserves over te houden, zou dat voordelig kunnen zijn. Ze zouden het kunnen gebruiken om de eieren van te maken, om hun ingekrompen organen weer op te bouwen of als extra verzekering voor het geval er nog niks te eten is bij aankomst. Als de vogels pech hebben, is de toendra dan immers nog niet sneeuwvrij.

Om te weten te komen met welke conditie steltlopers aankomen na die lange vlucht, hebben we ze gevangen meteen na aankomst, in de nog winterse toendra. De steltlopers strijken dan neer op de schaarse sneeuwvrije plekken. Een probleem bij het vangen is dat het 24 uur per dag licht is en geijkte methoden zoals mistnetten werken dan niet. Daarom hebben we een lichtgewicht versie van het 'wilsternet' meegenomen. Dat is een slagnet waar in Friesland, vroeger voor de kost en tegenwoordig voor onderzoek, goudplevieren mee worden gevangen. Met geluidsopnamen van baltsende steltlopers en plastic lokvogels lokten we de vogels naar het net en wisten er een redelijk aantal te vangen. Later in het seizoen vingen we ook veel

soorten vogels op het nest, met een klapnetje. Op die manier konden we de conditie vergelijken tussen vogels net na aankomst en tijdens het broeden. De variatie in aankomstgewichten van



de vers aangekomen vogels was erg groot, maar gemiddeld genomen waren alle soorten lichter dan later in het seizoen wanneer ze op het nest zaten. Ze waren bij aankomst wel een stuk zwaarder (3-18%) dan midden in de winter, wanneer ze in hun Afrikaanse overwinteringsgebieden zijn. Het restant van de voorraden waarmee ze in Taimyr aankomen bleek groot genoeg te zijn om 1 tot 2.5 dag zonder voedsel te overleven. Doordat we ook de samenstelling van de reserves (de verhouding tussen vet en eiwit) hebben bepaald (met behulp van deuteriummetingen waarmee het watergehalte van het lichaam bepaald wordt), weten we dat de gewichtstoename tussen aankomst en broeden vooral veroorzaakt wordt door een toename van eiwit, niet van vet. Uit andere studies aan de isotopensamenstelling van eieren is bekend dat de aanmaak van eieren meestal niet gebeurt met stoffen die nog uit de overwinteringsgebieden stammen. Daarom is het meest waarschijnlijk dat de reserves bij aankomst vooral gebruikt worden om de eerste dagen door te komen en om de organen weer op te bouwen. Een soort overlevingspakket dus.

Chapter 3



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

Unpublished manuscript

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 diameter² 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).

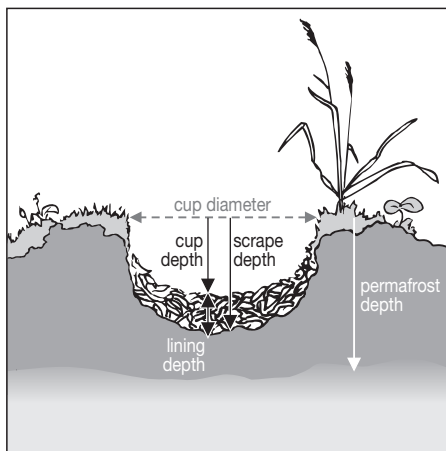


Figure 3.1. Illustration of nest cup measurements.

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 $T_{\text{egg}} = T_a + (T_i - T_a) \exp(-C \times \text{time})$ 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 $0.64 \times 10^{-3} \text{ s}^{-1}$ 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 (cup depth/diameter²) as the predictor variable instead of cup depth. This yields the equation: gradient = (0.29-0.29 x (cup depth/diameter²))x10³.

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, *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.

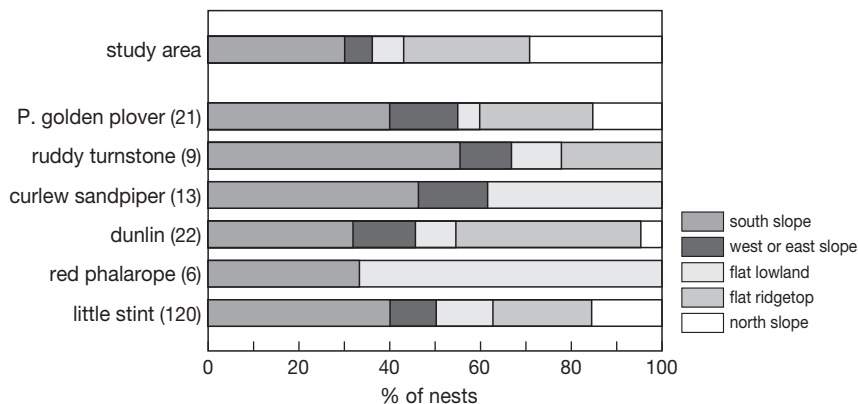
An estimate of the combined effect of these three nest features on nest insulation was derived by multiplying the proportional differences in egg cooling coefficient between the measured nest and an average pectoral sandpiper nest for each of the effects described above, with the value of C predicted 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 + day² 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, $H_5 = 4.08$, $P = 0.54$), 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, $P < 0.001$; day²: Wald = 34, $P < 0.001$; species: Wald = 15, $P = 0.006$; day.species: NS; day².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} ($F_{1,4} = 0.58$, $P = 0.487$).

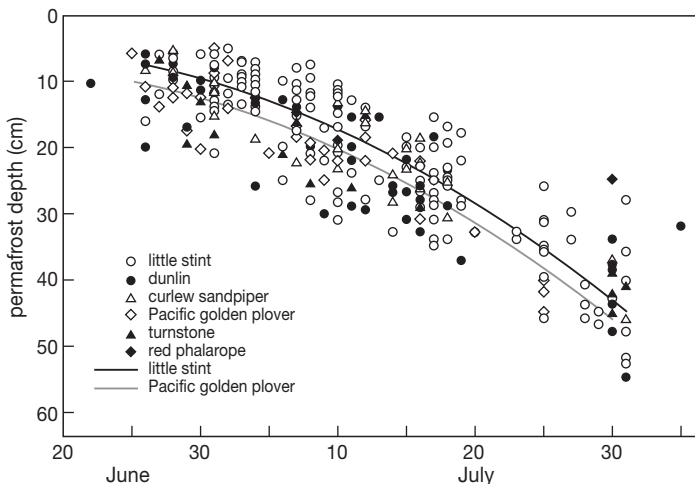
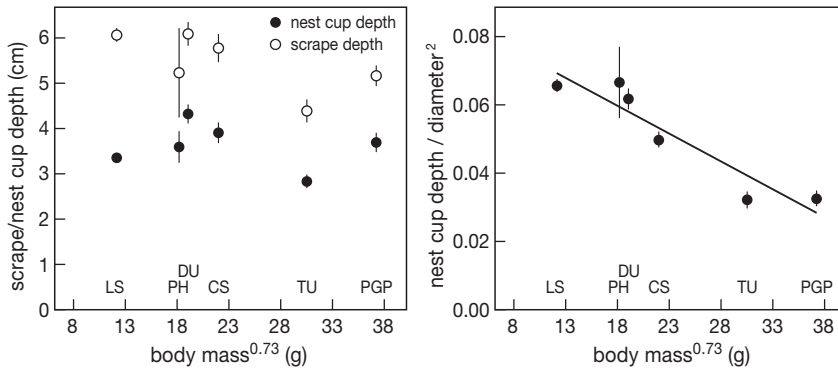


Figure 3.3. Depth of permafrost in relation to date in six species. The regression lines for the two extremes are given.

Figure 3.4. Nest cup and scrape depth (left) and nest cup depth/diameter² (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 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 ($F_{1,4} = 35.42$, $P = 0.0004$, $R^2 = 87.3$) 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/diameter¹*diameter² significantly increased with body mass^{0.73} ($F_{1,4} = 7.02$, $P = 0.057$, $R^2 = 54.6$, figure 3.4 right).

Figure 3.5. Nest lining depth (left) and nest lining dry mass (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.

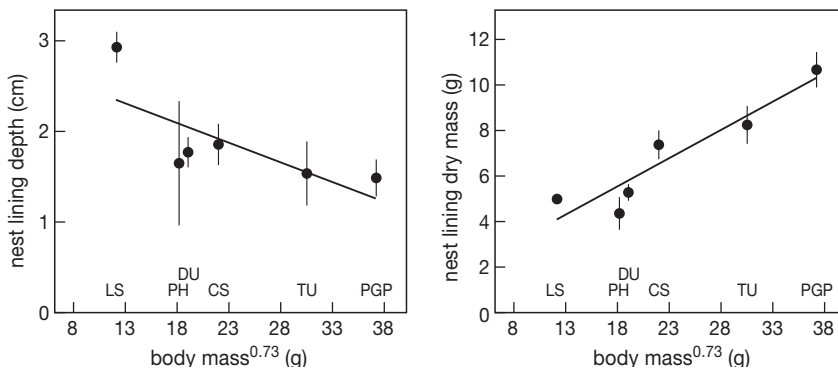


Figure 3.6. Nest lining material used by six different shorebirds with number of nests in brackets.

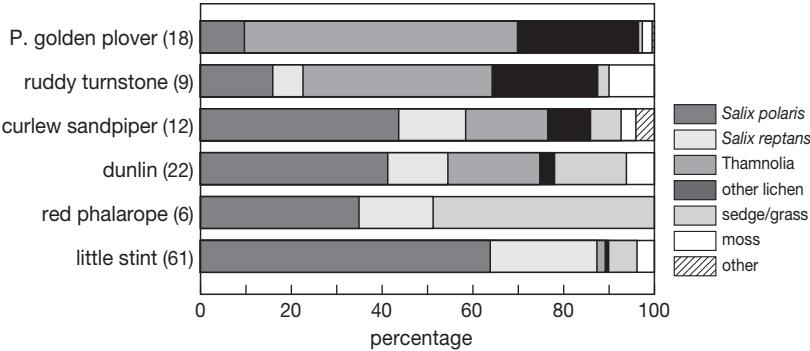
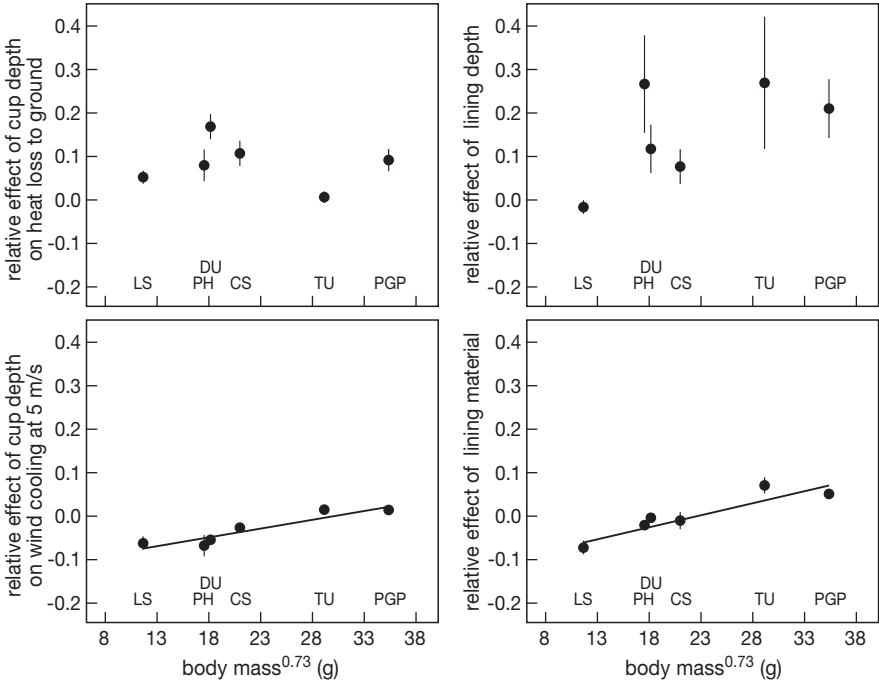


Figure 3.7. The relative contribution of cup depth to heat loss to the ground (upper left), of cup depth on wind cooling at 5 m/s (lower left), of lining depth (upper right) and of lining material (lower right) to egg cooling rates in relation to body mass. LS = little stint, PH = red phalarope, DU = 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 *Thammodia 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 ms⁻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/s, 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.

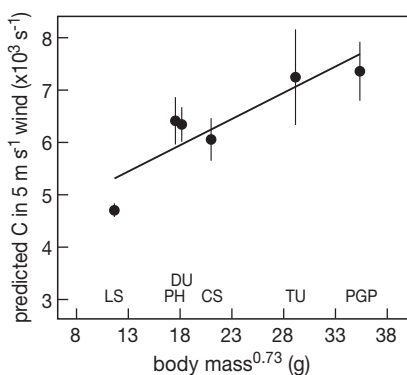


Figure 3.8. The predicted egg cooling coefficient in wind of 5 m/s in relation to body mass^{0.73}. LS = little stint, PH = red phalarope, DU = dunlin, CS = curlew sandpiper, TU = turnstone, PGP = Pacific golden plover. Average and SE values are represented for each species.

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 micro-climates 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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Eieren in de vriezer

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 diepgevroren 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.

Toch lukt het de broedende ouders om de eieren tot bijna 40°C te verwarmen. Omdat we wilden weten hoe steltlopers dat klaarspelen, hebben we diverse metingen aan de nestkuil verricht. Om te beginnen legden alle zes onderzochte soorten hun nesten op relatief warme plekken zoals zuidhellingen. Op de open toendra waar de Noordenwind koude poollucht aanvoert kan dat al veel schelen. Verder verschilt het ontwerp van de nestkuilen van de verschillen soorten nogal; met name in vorm en nestbekleding. Hoe kleiner de soort hoe meer werk ze van het nest maken en hoe dikker de nestbekleding. Kleine strandlopers maken relatief diepe, nauwe nestkuiltjes, die bekleed zijn met een dikke laag bestaande uit het best isolerende materiaal dat er op de toendra te vinden is: wilgenblaadjes. Die blaadjes zijn weliswaar in grote aantallen aanwezig, maar evenzogoed moeten de vogels ze allemaal naar de nestkom brengen. Dat doen ze door de blaadjes één voor één op te pikken en richting nestkom te gooien. Nieuwsgierig naar hoe vaak ze zo'n actie moeten uitvoeren, hebben we van vier nesten het aantal blaadjes geteld. De één tot zes cm dikke laag bleek uit wel 1000 tot 2000 blaadjes te bestaan! Grotere soorten zoals de steenloper en goudplevier maken ondiepere wijdere nesten die minder dik bekleed zijn met wat kostmossen en grassen. Die verschillende nesteigenschappen blijken door te werken in de isolerende werking en door die aanpassingen wordt het warmteverlies juist bij kleine soorten zoveel mogelijk beperkt. Voor die soorten is dat ook erg belangrijk omdat ze relatief veel energie uitgeven doordat de oppervlakte van hun lichaam klein is ten opzichte van de inhoud. Blijft natuurlijk de vraag waarom grotere soorten dan niet evenveel moeite doen om het warmteverlies te beperken. De grotere soorten zijn in onze studie ook toevallig de soorten waarbij beide ouders broeden en waarbij het nest zelden alleen gelaten wordt. Bovendien zijn hun eieren groter

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.

Chapter 4



Ingrid Tulp

Hans Schekkerman

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.

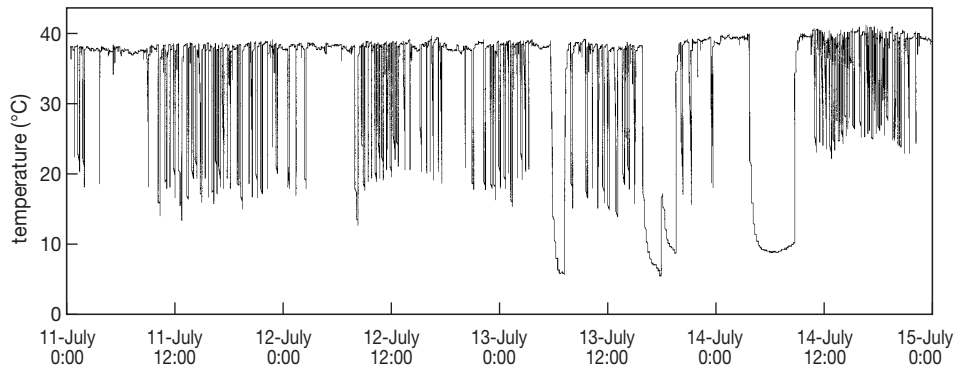
Weather data

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.

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.

species	body mass (g)	SD	N	clutch mass (g)	ratio
little stint (LS)	29.2	2.6	213	24	0.82
red phalarope (RP)	51.1	6.8	6	36	0.70
pectoral sandpiper (PS)	63.3	4.6	9	52	0.82
curlew sandpiper (CS)	64.7	4.2	28	48	0.74

Figure 4.1. Example of incubation pattern in little stint: the regular pattern is interrupted with three long periods of absence. Only a four day section of the total measurement is shown. The continuous nocturnal incubation periods are clearly visible.



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 hour¹, hour² and hour³ 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 *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.

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 (\pm SD) of recesses (top), mean recess length (middle) and total recess time (lower) in the four species in relation to time of day.

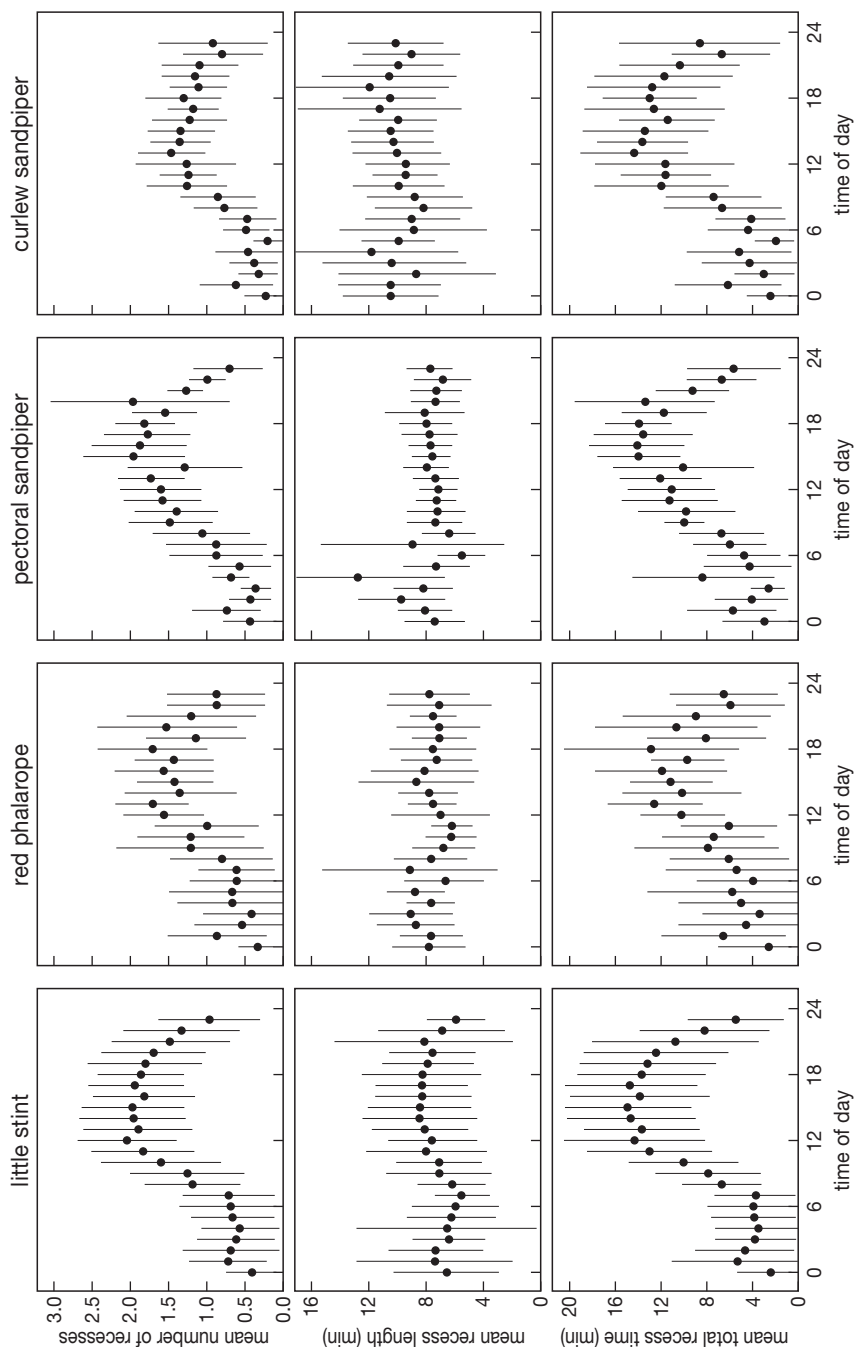


Table 4.2. Summary of incubation rhythms based on 24 h measurements. Total recess time (% of day absent from nest), mean recess length (minutes) and mean number of recess periods per day are presented for each species. Number of measurements per nest varied between 1-16 for LS, 6-7 for RP, 1-14 for PS and 1-18 for CS. During some measurements exceptionally long recesses took place. Analyses were performed both including ('full data') and excluding 24 h measurements with long absences ('reduced data').

species	full data including 'long absences'				N day	N nest	reduced data excluding 'long absences'				N day
	avg	SD	min	max			avg	SD	min	max	
little stint											
total recess time	18.8	7.7	4.7	57.6	197	38	17.4	5.8	4.7	43.6	179
recess length	9.4	8.6	3.5	86.9			7.8	4.3	3.5	39.1	
n recess/day	33.5	9.7	5.0	65.0			34.6	9.2	6.8	65.0	
red phalarope											
total recess time	13.1	2.0	10.8	16.9	13	2	see including 'long absences'				
recess length	7.2	1.0	6.1	9.4			(no long absences recorded)				
n recess/day	26.5	4.4	21.6	36.5							
pectoral sandpiper											
total recess time	17.1	5.7	9.5	40.5	64	7	15.9	3.8	9.5	27.3	59
recess length	9.8	9.0	4.5	63.4			7.7	2.1	4.5	14.6	
n recess/day	29.9	9.2	8.0	53.0			30.9	8.3	15.5	53.0	
curlew sandpiper											
total recess time	17.6	6.9	7.6	42.0	91	15	16.0	4.9	7.6	29.9	82
recess length	15.3	19.5	4.7	155.3			10.6	3.4	4.7	22.4	
n recess/day	21.6	7.4	3.9	45.9			22.8	6.6	11.8	45.9	

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).

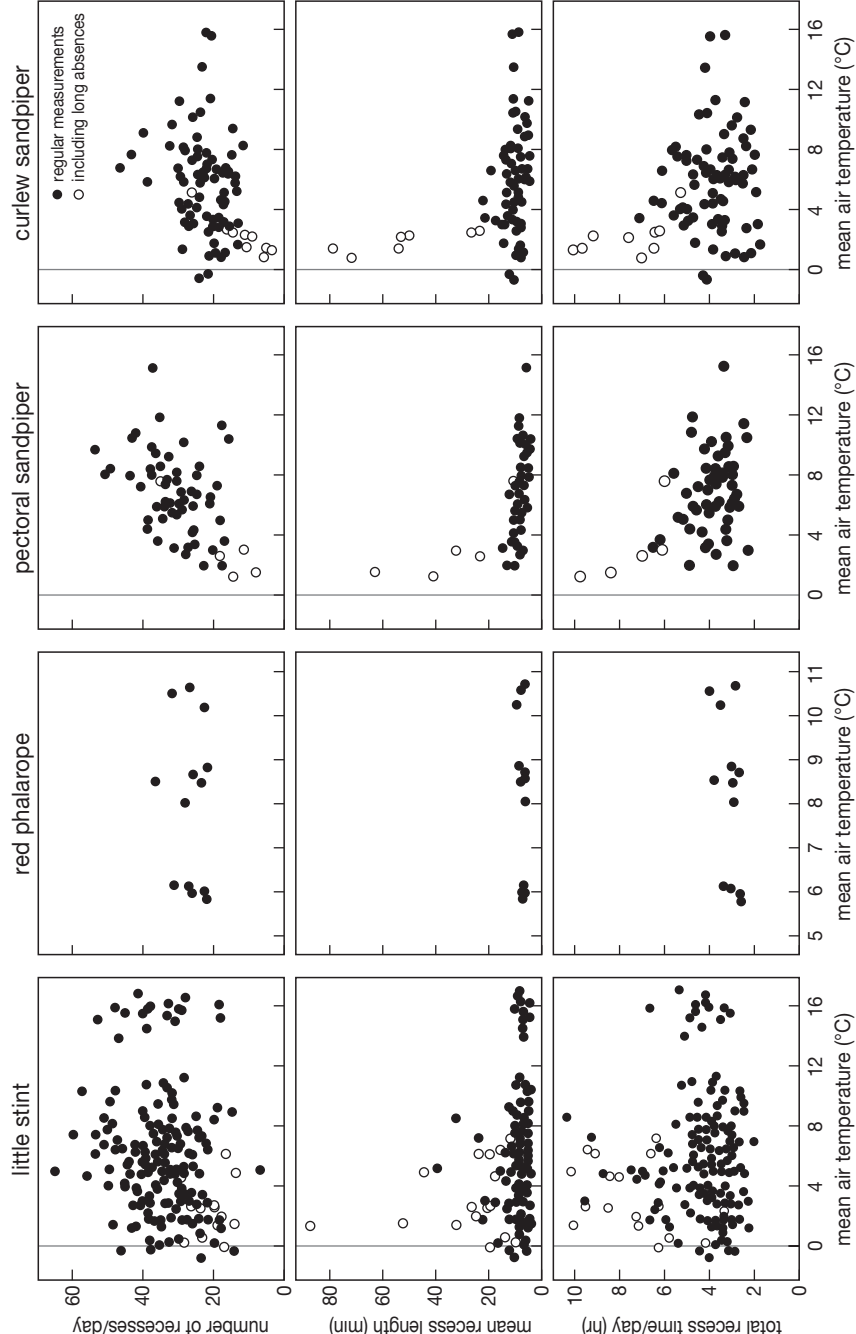


Table 4.3. Results of REML (Residual Maximum Likelihood, Linear Mixed Model) analyses of the incubation rhythm based on the reduced dataset (see table 4.2 for definition). Nest was entered as a random term. Three different response variables were used: proportion of day absent, number of recesses per day and mean recess duration. For RP none of the variables tested were significant.

species	response variable	fixed effect	Wald statistic	df	P	N	effect
little stint	total recess time	air temp	5.41	1	0.020	179	-
		n recesses/day	wind speed	30.80	1	<0.001	179
		precipitation	16.00	1	<0.001		+
	recess length	air temp	18.29	1	<0.001	179	-
		wind speed	29.34	1	<0.01		+
pectoral sandpiper	total recess time	incubation day	6.99	1	0.008	59	+
		air temp	4.32	1	0.038		-
	n recesses/day	air temp	10.80	1	0.001	59	+
		wind speed	10.37	1	0.001		-
		precipitation	15.58	1	<0.001		+
	recess length	air temp	15.25	1	<0.001	59	-
		precipitation	4.31	1	0.038		-
		curlew sandpiper	total recess time	no significant effect			
n recesses/day	precipitation		19.83	1	<0.001	82	+
	wind speed		14.47	1	<0.001		-
recess length	air temp		6.56	1	0.010	82	-
	precipitation		7.16	1	0.007		-
	wind speed		4.50	1	0.034		+

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.

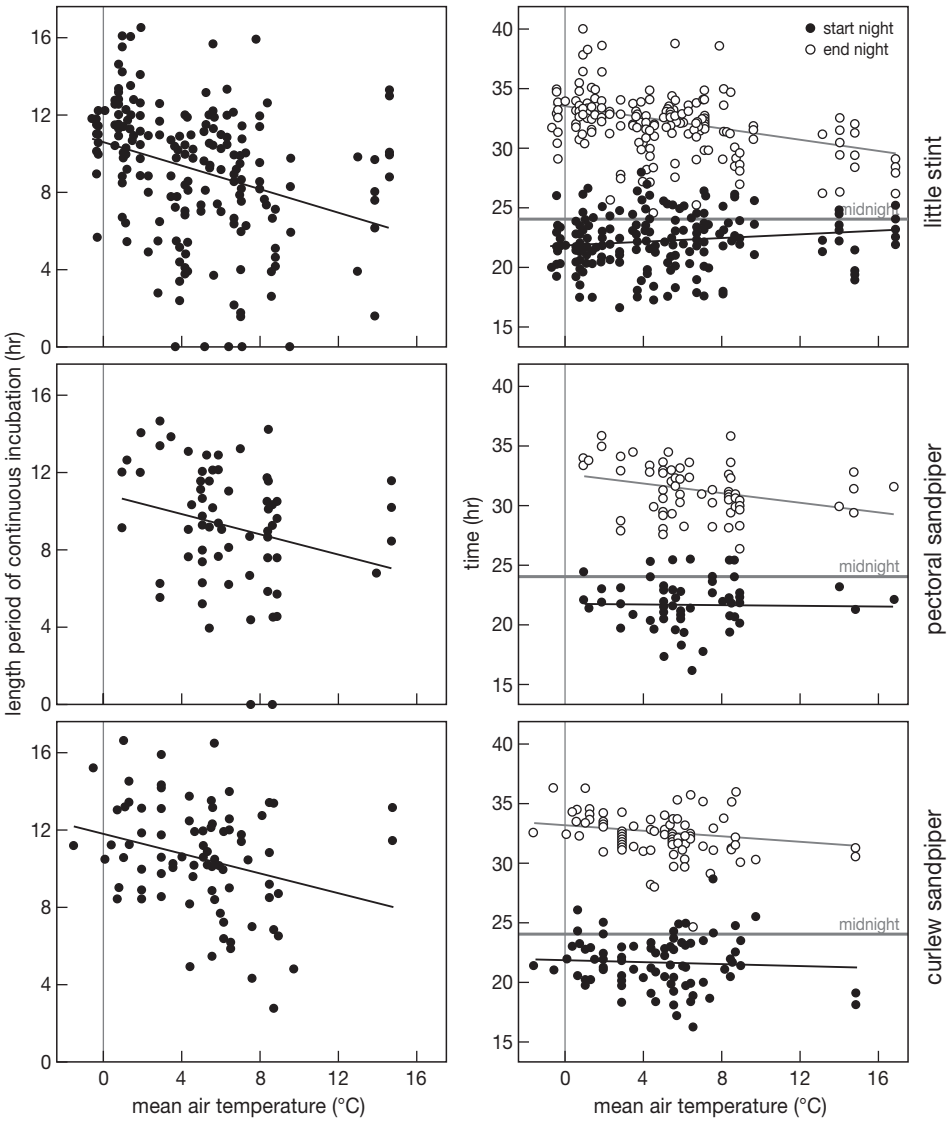


Table 4.4. Results of REML analyses of interspecific patterns in incubation rhythms for full and reduced dataset separately. See table 4.2 for definition full and reduced dataset.

response variable	fixed effect	Wald statistic	df	P	effect
full dataset					
total recess time	air temp	34.82	1	<0.001	-
	wind speed	18.65	1	<0.001	+
n recess/day	air temp	38.25	1	<0.001	+
	wind speed	81.84	1	<0.001	-
	precipitation	37.81	1	<0.001	+
recess length	species	33.00	3	<0.001	LS > PS > RP > CS
	air temp	81.59	1	<0.001	-
	wind speed	84.66	1	<0.001	+
	precipitation	5.81	1	0.023	-
reduced dataset					
total recess time	air temp	9.28	1	0.002	+
n recess/day	air temp	12.36	1	<0.001	+
	wind speed	46.59	1	<0.001	-
	precipitation	39.72	1	<0.001	+
recess length	species	38.58	3	<0.001	LS > PS > RP > CS
	air temp	37.45	1	<0.001	-
	wind speed	31.23	1	<0.001	+
	precipitation	8.95	1	0.003	-
	species	7.46	3	0.059	LS < PS < RP < CS

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

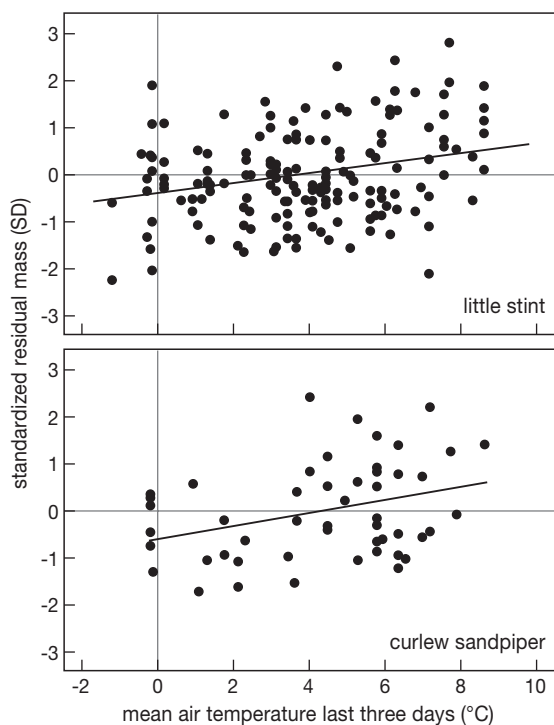


Figure 4.5. Residual (standardized) body mass of little stints and curlew sandpipers (after correction for wing length) in relation to the best explaining weather-related variable (mean temperature on the last three days before catching)

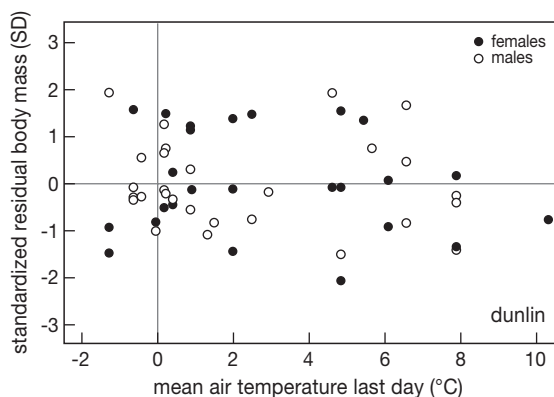


Figure 4.6. Residual (standardized) body mass (after correction for wing length) in male and female dunlin in relation to the best explaining weather-related variable (mean temperature on the day before catching).

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 $F_{1,48} = 6.26$, $P = 0.016$, $R^2 = 0.17$) 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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Druk, druk, druk, alleenstaande ouders in tijdnood

Onder steltlopers komen allerlei 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 uitbroeden 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 van het nest 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 het 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 urenlang 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 voorraadjie 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.

Chapter 5



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Body mass patterns of little stints at different latitudes during incubation and chick-rearing

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Due to the 'double-clutch' mating system found in the arctic-breeding little stint *Calidris minuta*, each parent cares for a clutch and brood alone. The resulting constraint on feeding time, combined with the cold climate and a small body size, may cause energetic bottlenecks. Based on the notion that mass stores in birds serve as an 'insurance' for transient periods of negative energy balance, but entail certain costs as well, body mass may vary in relation to climatic conditions and stage of the breeding cycle.

We studied body mass in little stints in relation to breeding stage and geographical location, during 17 expeditions to 12 sites in the Eurasian Arctic, ranging from N-Norway to NE-Taimyr. Body mass was higher during incubation than during chick-rearing. Structural size, as estimated by wing length, increased with latitude. This was probably caused by relatively more females (the larger sex) incubating further north, possibly after leaving a first clutch to be incubated by a male further south. Before and after correction for structural size, body mass was strongly related to latitude during both incubation and chick-rearing. In analogy to a similar geographic pattern in overwintering shorebirds, we interpret the large energy stores of breeding little stints as an insurance against periods of cold weather which are a regular feature of arctic summers. Climate data showed that the risk of encountering cold spells lasting several days increases with latitude over the species' breeding range, and is larger in June than in July. Maintaining these stores is therefore less necessary at southern sites and during the chick-rearing period than in the incubation period. When guarding chicks, feeding time is less constrained than during incubation, temperatures tend to be higher than in the incubation period, reducing energy expenditure, and the availability of insect prey reaches a seasonal maximum. However, the alternative interpretation that the chick-tending period is more energetically stressful than the incubation period, resulting in a negative energy balance for the parent, could not be rejected on the present evidence.

Introduction

The way in which energy stores are regulated in birds is often interpreted to be the result of a trade-off between the risk of starvation and certain costs involved in carrying stores (Lima 1986; Houston and McNamara 1993; Lovvorn 1994; Gosler et al. 1995; Slagsvold and Johansen 1998). Although empirical evidence that heavier birds are more prone to predation than lean ones is limited and not universal (Whitfield et al. 1999), maintaining excess energy stores and carrying them around is energetically costly (Bruinzeel and Piersma 1998). Whether the costs are paid as increased work load or increased predation risk, a bird is not expected to maintain energy stores unless they are functionally adaptive. Wintering waders in temperate regions show marked variation in midwinter body mass and in organs indicative of condition (Pienkowski et al. 1979; Davidson et al. 1986a; Davidson et al. 1986b; Summers et al. 1992; Piersma et al. 1994; Zwarts et al. 1996). In colder areas dunlins *Calidris alpina* and sanderlings *Calidris alba* carry larger fuel stores than in more benign climates (Castro et al. 1992; Piersma et al. 1994). This pattern has been explained as a latitude-related insurance for periods of negative energy balance caused by high energy expenditure and/or reduced availability of food. The risk of encountering inclement weather is generally higher in colder areas, and therefore the insurance needs are greater.

Breeding in the Arctic is energetically costly due to low temperatures, especially for small birds with open nests (Piersma and Morrison 1994). Additionally, incubation duties strongly reduce the time available for feeding. The large short-term variations typical of arctic weather result in large variations in food availability. Therefore birds breeding at higher latitudes may be more likely to suffer shortfalls in energy budgets, similar to overwintering waders.

The little stint *Calidris minuta* is the smallest wader breeding in the High Arctic and provides a good model to study the implications of breeding at low temperatures. In the double-clutch mating system found in this species (Hildén 1978; Chylarecki and Kania 1992; Tomkovich et al. 1994), both males and females incubate a clutch by themselves. During incubation, the birds regularly leave the nest to feed, since their energy reserves do not suffice for the complete 20-21 day incubation period. The resulting trade-off between incubation and foraging is influenced by weather conditions (Cartar and Montgomerie 1985; chapter 4)

Because time available for feeding is more severely constrained during incubation than when tending the self-feeding chicks (chapter 6), and because the climatic difficulties are expected to increase with breeding latitude, we predicted that 1) little stints should maintain larger stores during incubation than during chick-rearing, and 2) northerly breeding birds should be heavier than southerly breeding birds. In this paper we test these predictions while taking into account the potentially confounding effects of structural size and sex ratios. Furthermore we explore the risks of encountering periods of adverse weather at different latitudes within the Eurasian arctic.

Methods

Data on little stints were collected during 17 expeditions to 12 sites between 1976 and 1998: ten sites in the typical and arctic tundra subzones (Chernov 1985) on the Taimyr Peninsula in Russia and two in the southern tundra subzone in northern Norway (table 5.1, figure 5.1). Detailed descriptions of the sites and breeding conditions are given elsewhere (Hildén 1978; Hildén 1988; Tomkovich and Vronsky 1988b; Tomkovich and Vronsky 1988a; Summers et al. 1989; Tomkovich et al. 1994; Tomkovich and Vronsky 1994; Prokosch and Hötter 1995;

Table 5.1. Overview of study sites and sample sizes. The numbers refer to figure 5.1 (OH=Olavi Hildén, RS=Ron Summers, PC = Przemek Chylarecki, AS = Arkadiusz Sikora, MS = Mikhail Soloviev, IT = Ingrid Tulp, LB = Leo Bruinzeel, WK = Woiciech Kania, PT = Pavel Tomkovich, WWF = Worldwide Fund for Nature Germany, KD = Klaas van Dijk, PV = Peter Venema, HS = Hans Schekkerman, MR = Marc van Roonen). Ntot represents the total number of weighings before and after hatching. The median start of incubation and the distance to the closest weather station for each location are given in the last three columns.

nr	location	year	latitude	longitude	Ntot	Nincu	Nchick	observer	median start incubation	closest weather station	distance (km)
1	Varanger peninsula	Norway	1976-89	70°32' N	30°34' E	36	34	2	OH	Sletnes	105
2	Nordkinn-Halvøya	Norway	1989	71°07' N	27°40' E	39	24	15	RS	Sletnes	20
3	Sibiryakov Island	Taimyr	1990	72°44' N	79°08' E	30	25	5	PC & AS	Dikson	98
4	Khatanga River mouth	Taimyr	1994-98	72°51' N	106°02' E	61	49	12	MS	Khatanga	154
5	Medusa Bay	Taimyr	1996	73°20' N	80°30' E	99	83	16	IT & LB	Dikson	23
6	Malaya Logata R. mouth	Taimyr	1989	73°25' N	98°25' E	20	20	0	WK	Khatanga	208
7	Uboinaya River	Taimyr	1984	73°37' N	82°20' E	18	2	16	PT	Dikson	62
8	Pyasina River mouth	Taimyr	1990	74°07' N	86°50' E	50	46	4	WWF	Cape Sterlegov	154
	Pyasina River mouth	Taimyr	1991	74°07' N	86°50' E	60	58	2	PC & WK		
	Pyasina River mouth	Taimyr	1993	74°07' N	86°50' E	72	57	15	KD & PV		
9	Lake Pronchishchev	Taimyr	1991	75°16' N	112°28' E	25	6	19	HS & MR	Cape Chelyuskin	344
10	Lenivaya River	Taimyr	1983	75°16' N	89°35' E	53	24	29	PT	Cape Sterlegov	27
11	Cape Sterlegov	Taimyr	1990	75°26' N	89°08' E	18	17	1	WWF	Cape Sterlegov	7
	Cape Sterlegov	Taimyr	1994	75°26' N	89°08' E	10	5	5	HS & IT		7
12	Knipovich Bay	Taimyr	1990	76°04' N	98°32' E	47	36	11	PT & MS	Cape Chelyuskin	234
	Knipovich Bay	Taimyr	1991	76°04' N	98°32' E	36	36	0	OH		
total					674	521	153				

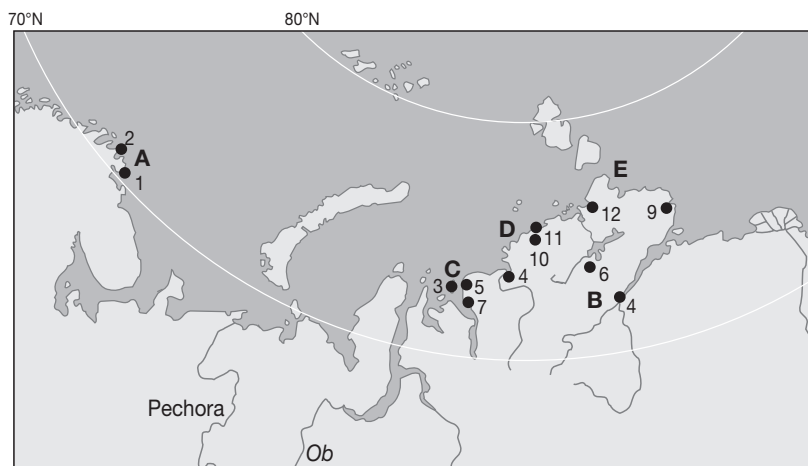
Schekkerman and van Roomen 1995; Tulp et al. 1997; Tulp et al. 1998). The study periods usually comprised June and July and in some cases early August.

During the incubation and early chick-rearing stages, little stints were caught by using a small clap net, pull net, walk-in trap or mist-net. Incubating birds were caught on the nest and birds tending young were caught brooding. Birds were ringed, and weighed with a spring balance, in most studies to the nearest 0.1 g or 0.5 g, but on Sibriakov Island to the nearest 1.0 g. Wing length (maximal chord) was measured using a stopped rule (1 mm). At Lake Pronchishchev in 1991 and Medusa Bay in 1996, up to four repeated weighings of the same birds were collected. Except where explicitly testing for variation within individuals only one measurement per bird in each phase (selected randomly) was included in the analyses.

Little stints show little or no sexual plumage dimorphism. Since female little stints are on average slightly larger than males, patterns in body mass might be confounded by variation in sex ratios. We refrained from using body size to allocate birds to a sex as this would give erroneous results if there is geographic variation in size. At some sites a sub-sample of the birds was sexed by several methods: (1) behavioural observations of colour-marked birds during copulation; (2) the size of the cloaca (egg laying and early incubation stages only, see Tomkovich (1991) and Soloviev and Tomkovich (1995); (3) examination of the gonads in collected specimens.

A large number of observers collected measurements and this could introduce bias. Some observers worked together at a site and standardized their measurement techniques. Underhill et al. (unpubl. data) using the same data set as presented in this paper, tested for differences between observers, and found that though significant the discrepancies were small. The largest difference between the mean wing length for an observer and the overall mean was 0.7 mm (3 %). Since most of the measurements were taken by a few observers who worked both in northern and southern sites (table 5.1), we do not think that observer effects biased the latitudinal effects described in this paper.

Figure 5.1. Map of study locations (numbers) and weather stations (letters, see tables 5.1 and 5.2 for coordinates).



Hatching date was derived from direct observations of hatching or egg-laying, flotation of eggs, or chick measurements, using an incubation period of 20 days (after clutch completion, Cramp and Simmons 1983). For some birds, no information on date relative to hatching was known, other than whether the bird was incubating or had chicks. These data were used in analyses in which only the phase in the breeding cycle was included. Since not all data sets are equally complete, some analyses could only be carried out on subsets of the total data (indicated where applicable). Statistical analyses were carried out using Genstat 5.0 (Genstat 1993) and significance accepted at $P = 0.05$.

Long-term climate data were not available from the study sites themselves, but data from four weather stations in the Russian Arctic and one in northern Norway were used instead (table 5.2, figure 5.1). Mean temperature and wind speed for Taimyr in the period 1994-1997 were taken from the Internet (<http://www.ncdc.noaa.gov>). For one of the Russian stations, Cape Sterlegov, data were only available for 1994 and were supplemented with published data from 1989 and 1990 (Prokosch and Hötter 1995). The weather station at Slettnes in northern Norway provided data from this site for 1989-1996. Because we are interested in how often days with weather causing an energy imbalance for incubating little stints occur, we have analysed how many days the mean temperature stayed below 1°C in June and July. Body mass of little stints at Medusa Bay declined when the air temperature remained below 1°C on three consecutive days (Tulp et al. unpubl. data).

Table 5.2. Locations of the weather stations from which weather data were taken. The letters refer to the map in Figure 5.1. Data given for June and July represent the whole months. In the last four columns the probabilities of a cold spell with temperature $< 1^{\circ}\text{C}$ lasting three days in the period 20 June-20 July and June and July are given.

location	latitude	longitude	mean air temp. ($^{\circ}\text{C}$)		mean wind sp. (m/s)		probability of cold spell ≥ 3 days		
			June	July	June	July	20 June-20 July	June	July
A Slettnes	71°05'N	28°13'E	6.1	8.8	6.4	5.9	0.00	0.00	0.00
B Khatanga	71°59'N	102°27'E	4.5	13.4	4.9	4.2	0.00	0.26	0.00
C Dikson	73°32'N	80°24'E	0.0	5.1	6.4	5.7	0.11	0.70	0.03
D Cape Sterlegov	75°24'N	88°47'E	-0.7	3.1	5.9	5.1	0.35	0.63	0.20
E Cape Chelyuskin	77°43'N	104°18'E	-1.7	1.3	6.1	5.3	0.60	0.85	0.44

Table 5.3. Mean body mass (with standard errors) in the six studies of which at least six measurements were available both in the incubation and the chick-rearing period.

nr	location	incubation			chick-rearing			Student's t-test	
		mean	SD	N	mean	SD	N	t	P
2	Nordkinn-Halvøya	28.3	0.3	24	24.6	0.5	15	6.71	< 0.001
4	Khatanga River mouth	28.8	0.4	49	24.9	0.6	12	4.36	< 0.001
8	Pyasina River mouth	29.3	0.3	57	26.6	0.7	15	3.58	< 0.001
9	Lake Pronchishev	32.4	0.9	6	28.6	0.6	19	3.04	0.006
10	Lenivaya River	31.5	0.7	24	27.9	0.4	29	4.61	< 0.001
12	Knipovich Bay	31.4	0.4	36	27.9	0.5	11	4.82	< 0.001

Results

Body mass and size

Before investigating any relationship between body mass and latitude or breeding phase, a correction for structural size needs to be made. Because we cannot assume a priori that the relationship between size and body mass is linear, we regressed the logarithm of body mass on the logarithm of wing length across all studies. Log wing length explained a significant part of the variation in log body mass ($F_{1,663} = 120$, $P < 0.001$, $R^2 = 0.15$). The wing length exponent (1.16, $SE = 0.11$) did not differ significantly from 1, indicating that body mass was linearly related to wing length. When latitude and stage of the breeding cycle were included in the model first, the wing length exponent (1.10, $SE = 0.11$) still did not differ from 1. Therefore, wing length (linear) was used as the indicator of structural size in all further analyses.

Figure 5.2. Body mass in relation to incubation stage at six sites for which at least six data points before and after hatching were available. 0 represents the day of hatching, negative values are prior to hatching, positive values after hatching.

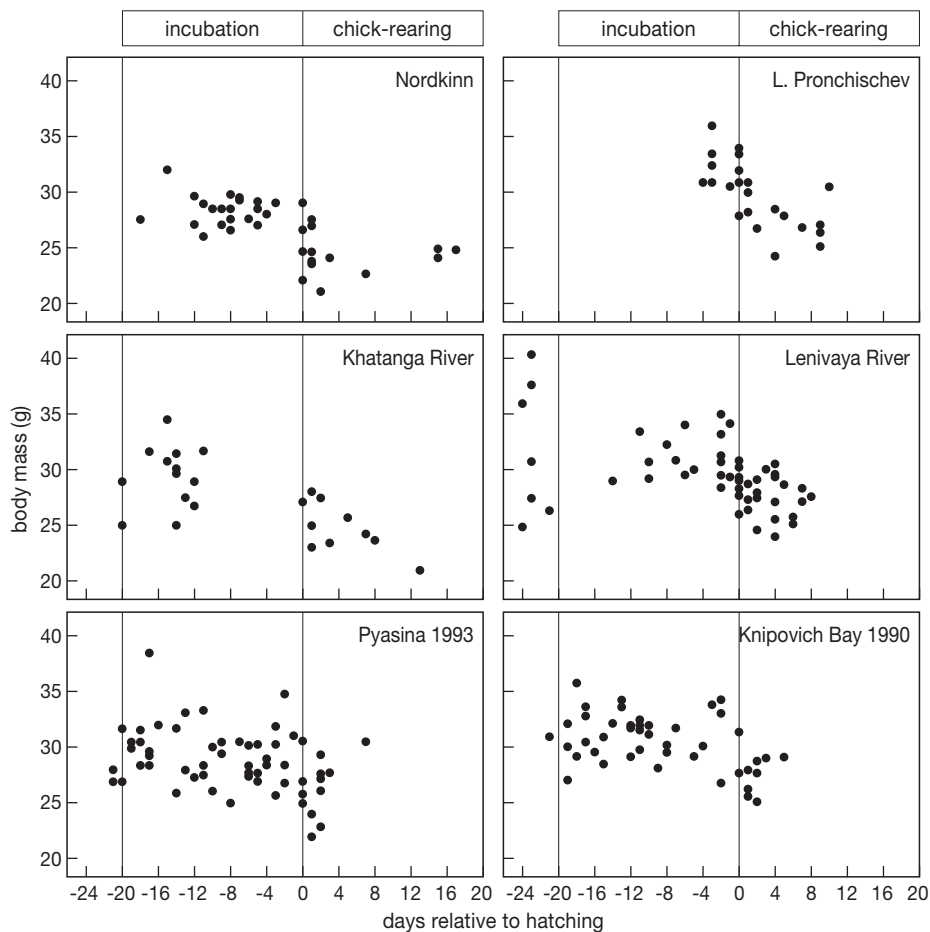
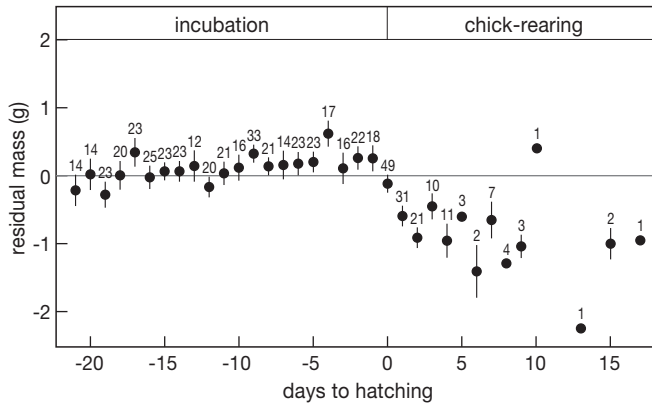


Figure 5.3. Residual mass, after correction for wing length and site/year in relation to the time of hatching. Numbers indicate sample sizes.



Body mass and phase of breeding cycle

For six sites, at least six body mass measurements both before and after hatching were available (figure 5.2). At the Lenivaya River, seven individuals were caught in the egg-laying phase; four very light birds had just laid an egg, while three extremely heavy ones were caught presumably just before egg-laying. As they fall outside the scope of this paper the measurements of (pre)laying birds were excluded from all analyses.

In all six datasets containing mass before and after hatching, mean body mass was significantly higher before than after hatching (figure 5.2, table 5.3). In a two-way ANOVA on the combined data using wing length as a covariate ($F_{1,219} = 37.0$, $P < 0.001$), both the effects of phase ($F_{1,219} = 107.3$, $P < 0.001$), and location ($F_{5,219} = 9.44$, $P < 0.001$) were significant, while the interaction between phase and location was not ($F_{5,219} = 0.23$, $P = 0.95$).

To examine patterns in mass within each phase we used all birds from all sites for which an estimate of clutch hatching date was available, and plotted the residual mass, after accounting for the effect of structural size (wing length) and site/year in an ANCOVA, against days relative to hatching (figure 5.3). Body mass was stable throughout the incubation period (linear regression of residual mass on dth, $F_{1,421} = 1.73$, $P = 0.189$). Starting on the hatching day, mass decreased strongly for 4–6 days, after which it slowed down (figure 5.3). Because of this decline, the mean body mass in the chick-rearing period (table 5.3) can be affected by differences between the datasets in timing of catching relative to hatching.

In figures 5.2 and 5.3, measurements before and after hatching only occasionally represent the same individuals. In the studies where some individuals were captured repeatedly (Medusa Bay, Lake Pronchishchev, and Pyasina River mouth), 12 out of 13 individuals that were caught both during incubation and chick-rearing, showed a marked decline in body mass between the incubation and chick-rearing periods (paired T-test, $t = 3.80$, $P = 0.003$). Differences between pre- and post-hatching mass ranged up to 6 g in the same individual. To test whether individuals lost body mass during incubation we carried out a paired t-test of incubating birds of which two weighings during incubation were available ($N = 36$). Body

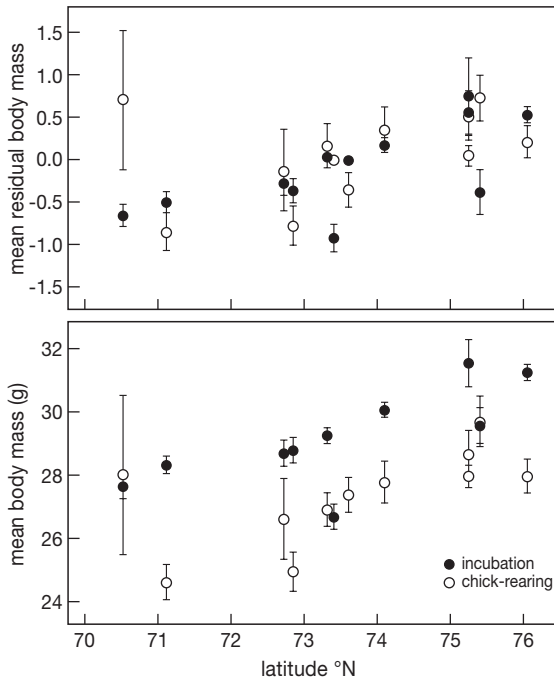


Figure 5.4. Mean body mass and mean residual body mass (with standard errors) in the incubation and chick-rearing period, relative to latitude. The hatching day is included in the posthatching period. Numbers on which this figure is based are given in table 5.1.

mass did not change significantly between two weighings during the incubation period (paired T-test, $t = 0.56$, $P = 0.579$). For nine birds (all Medusa Bay), two weighings during incubation and one during chick-rearing were available. The difference between the two weighings during incubation was significantly smaller than the difference between the last weighing during incubation and the weighing during chick-rearing (weighings 5 to 10 days apart, paired T-test, $t = 2.35$, $P = 0.043$, $N = 9$). Hence, repeatedly weighed individuals showed the same pattern as the full data: variation around a stable body mass during incubation, and a lower mass after hatching of the chicks.

Body mass and geography

During both incubation and chick-rearing, birds breeding at higher latitudes were heavier than more southerly breeders ($F_{1,663} = 79.48$, $P < 0.001$, figure 5.4). However, the structural size of the birds, represented by wing length, also showed a positive relationship with latitude ($F_{1,663} = 13.67$, $P < 0.001$). Thus, the latitudinal increase in body mass is confounded by a trend in size.

After correction for wing length, inclusion of both incubation phase ($F_{1,661} = 109$, $P < 0.001$) and latitude ($F_{1,661} = 76$, $P < 0.001$) still significantly improved the model explaining the variation in body mass ($R^2 = 0.34$). Two- and three-way interactions between wing length, latitude and incubation phase were not significant ($P = 0.632$ to 0.987). Hence northerly breeding little stints carry larger energy stores than birds breeding in the south of the range. Our data do not provide insight into the absolute size of these stores, as we did not determine body composition. To estimate store-free mass we therefore used the relationship between

wing length and body mass of little stints wintering in coastal West Africa (Zwarts et al. 1990, $y = 0.456x - 22.56$). These wintering birds are presumed to have constant mass and carry only about 8% fat on average (Piersma and van Brederode 1990; Zwarts et al. 1990). By subtracting estimated store-free mass from the observed mass, an estimate of the mass stored during incubation and chick-rearing was obtained. As was the case for body mass corrected for wing length, the estimated mass stores increased with latitude, both during incubation ($y = 0.522x - 31.65$, $F_{1,588} = 52.1$, $P < 0.001$), and chick-rearing ($y = 0.454x - 28.92$, $F_{1,152} = 12.53$, $P < 0.001$). At 70°N, predicted mean stores during incubation were 4.9 g, while at 76°N they were 8.0 g.

Patterns within sexes

The proportion of females among birds in our study sites, combined with the little information available in the literature (table 5.4), showed a significant increase with latitude (logistic regression, $\chi^2_1 = 7.93$, $P < 0.01$). This increase is still apparent if one considers only those sites where all or most birds were of known sex (2nd, 3rd, 5th, 8th site in table 5.4).

In the subsample of birds that were sexed, body mass was higher in females than in males, and increased with structural size (wing length) and latitude. (ANCOVA, wing: $F_{1,162} = 42.45$, $P < 0.001$, sex: $F_{1,162} = 11.96$, $P < 0.001$, latitude: $F_{1,166} = 16.73$, $P < 0.001$). The interaction terms between sex and structural size ($F_{1,162} = 2.58$, $P = 0.111$) and between sex and latitude ($F_{1,162} = 0.30$, $P = 0.585$) were not significant, indicating that the slopes of the relationships between mass and structural size and latitude were similar for males and females, but females were on average 2.9 g heavier than males. This might be due to larger stores in females, or to a difference in store-free mass other than that accounted for by wing length. The interaction between mass and structural size was not significant ($F_{1,162} = 0.45$, $P = 0.502$).

Table 5.4. Sex ratios of little stints caught on the nest at various sites, ordered by latitude. Birds were sexed according to cloaca size, behaviour, or gonadal inspection. Additional data are included on birds collected by Schaaning in Kozlova (1962)^a and Haviland (1915)^b.

nr	location	lat. °N	females	males	unknown	f/m
1	Varanger Peninsula	70°32'	8	12	16	0.7
	Novaya Zemla ^a	71°-73°	2	15	-	0.1
	Golchika ^b	72°50'	2	6	-	0.3
4	Khatanga River mouth	72°51'	11	2	48	5.5
8	Pyasina River mouth	74°07'	31	16	3	1.9
10	Lenivaya River	75°16'	6	5	42	1.2
11	Cape Sterlegov	75°26'	4	8	6	0.5
12	Knipovich Bay	76°04'	24	12	-	2.0
12	Knipovich Bay	76°05'	18	9	20	2.0

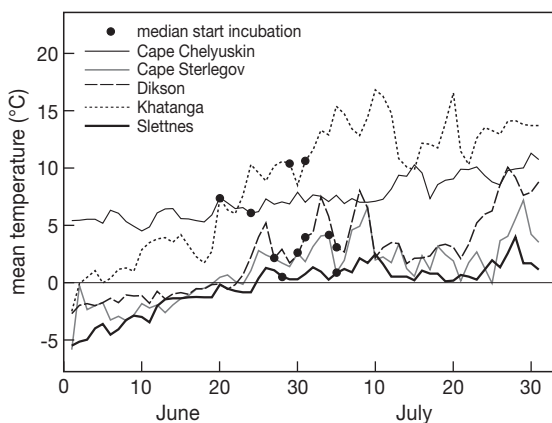


Figure 5.5. Mean temperature in the period 1994-1997 at four weather stations on the Taimyr Peninsula and one in northern Norway. Co-ordinates of the weather stations are given in table 5.2. The dots represent the median start of incubation observed at the twelve locations, placed on the temperature line for the closest weather station (see also table 5.1).

Weather

The sites from which weather data were available (table 5.2) comprise the same latitudinal/longitudinal range as where data on little stints were collected and are all situated well within the species' breeding range. Distances from each study site to the nearest weather station varied between 7 and 344 km (table 5.1). The mean temperature was lowest at Cape Chelyuskin in both June and July, the most northerly site, and highest at Slettnes in June and Khatanga in July, the southernmost sites (figure 5.5). Temperatures below 1°C occurred in Cape Chelyuskin on more than 50% of the days during the incubation period, but never at Slettnes and Khatanga. The risk of running into a period of three consecutive days with temperatures below 1°C was only apparent at Cape Chelyuskin, Cape Sterlegov and Dikson and higher in June than in July (table 5.2, figure 5.5). The onset of the breeding season showed little variation between locations: median start of incubation varied between 20 June and 5 July (figure 5.5). Although there was a slight tendency for earlier breeding at more southerly sites, this was not enough to compensate for the latitudinal effect on climate (figure 5.5).

As wind speed can be an important factor in energy costs of thermoregulation (Wiersma and Piersma 1994) we also investigated variation in wind speed among the different sites (table 5.2). Wind speed showed no clear trend and was influenced more by the distance to the open sea than by latitude or longitude, with lowest wind speeds occurring at Khatanga, situated far inland. Since little stints have deep nests, they are effectively sheltered when incubating.

Discussion

Three extremes: size, breeding area and incubation role

Birds living in the Arctic have to deal with a cold and capricious climate. The combination of low temperatures and the small size of little stints results in high energy expenditure in the incubation period (chapter 6). Apart from an increase in thermoregulation costs (Wiersma and Piersma 1994), during inclement weather the surface activity of tundra arthropods, the main food source of breeding little stints, is strongly reduced (Underhill et al. 1993; Schekkerman and van Roomen 1995; Schekkerman et al. 1998; Tulp et al. 1998; chapter 9). As male and female little stints carry out the incubation and chick-rearing duties for

one brood alone, this implies that the available time has to be divided between caring for offspring and safeguarding the parents' own energy balance. During incubation, little stints leave the nest for numerous short foraging bouts. When the sun is low (23:00h to 05:00h) the adults do not leave the nest for several hours (Tulp et al. 1997). In cold weather, little stints spend more time incubating and less time off the nest than in benign weather (Tulp et al. 1997), as has been shown in white-rumped sandpipers *Calidris fuscicollis* (Cartar and Montgomerie 1985) and several other wader species with uniparental incubation (Kondratyev 1982; Tomkovich and Fokin 1983). The variation in nest attendance creates some leeway in the little stint's time budget. Based on their own condition, the availability of food, the current weather, and the stage of incubation, they can decide how to allocate their time. Little stints are considerably heavier during the breeding period than at other stages in their yearly cycle, apart from short periods preceding long-distance migrations when they weigh up to 30-35 g (Zwarts et al. 1990; Meininger and Schekkerman 1994). Body mass measured during incubation amounts to 123-150% of the mass of birds wintering in coastal West Africa and the Mediterranean Sea (Zwarts et al. 1990; Van der Have 1997). These large energy stores might thus provide an insurance for periods of negative energy balance.

Body mass during incubation versus chick-rearing

We observed a decrease in body mass between the incubation and the chick-rearing periods, which was reported earlier by Schekkerman & van Roomen (1995) and Soloviev & Tomkovich (1997) for little stints and several other wader species, and which could be explained in several ways. First, the birds might simply be running out of energy stores because of a negative energy balance. In this case, a steady decline in mass during the incubation period would be expected, a pattern which was not found in this study (figure 5.3). In a study of this scope, with a great number of sites and years, some of the birds caught must have encountered cold spells, resulting in mass loss. The fact that this did not lead to a decrease in mean mass implies that birds can rapidly make up deficits, and indicates that energy balance can be positive at times during the incubation period.

Another possibility is that the hatching and chick-tending periods are more energetically stressful to the parent than the incubation stage, and a negative energy balance develops at or shortly after hatching. However, Kondratyev (1977) and Norton (1972) showed that nest attendance in western sandpiper *Calidris mauri*, dunlin, and pectoral sandpiper *Calidris melanotos* decreases during the last days of incubation. Although this indicates that feeding time increases at hatching, an alternative explanation could be that the adults are so energetically stressed that they reduce their reproductive effort to ensure survival. In addition, feeding time may be limited not only by requirements for incubation and brooding, but also by other behaviours such as vigilance, and (energetically costly) aerial defence of nest and young.

Alternatively, the sudden drop in mass could be adaptive. Once the chicks have hatched, time constraints on feeding for the parent might be lifted, because less time is needed for other behaviours than foraging or because foraging is compatible with tending chicks. The proportion of time devoted to incubation or brooding is 82% (chapter 4) when on eggs and decreases from 70% to 30% when brooding chicks of 1 to 8 days old (chapter 6). In addition, average temperature reaches a maximum in the chick-rearing period and the risk of encountering long periods of adverse weather is at a minimum (table 5.2, figure 5.5). Also, food supply peaks at this time, which further reduces the need for large energy stores as an insurance for periods of negative energy balance. If so, it would even be advantageous to

be lean (Freed 1981; Norberg 1981), because the costs of flight and terrestrial locomotion depend on body mass (Pennycuik 1989; Bruinzeel and Piersma 1998), and predation risk is expected to increase with the amount of reserve tissue (Lima 1986; Hedenström 1992; Houston and McNamara 1993; Witter et al. 1994; Gosler et al. 1995; van der Veen 1999). Also because little stints with chicks spend considerably more time in flight when alarming and distracting predators than when incubating eggs, they might benefit by disposing of unnecessary reserves. However, some stores may still be necessary to overcome bad weather when the chicks need to be brooded for long periods and arthropod availability is low. Mass loss during incubation may occur both under the 'energetic stress' and the 'adaptive' hypothesis.

During incubation, the risk of encountering a cold spell declines through June and early July (figure 5.5). In our study we did not find a concomitant decline in insurance levels. (Schamel and Tracy 1987), found a decline in body mass during incubation in another uniparental wader, the red phalarope *Phalaropus fulicarius*, especially in more northern areas. In small birds with uniparental incubation some studies show that birds retain body mass during incubation, while others find a decline (review in Williams 1996).

To distinguish between the 'stress' and the 'adaptive' explanations (which are not mutually exclusive) one could experimentally manipulate food intake or energy expenditure of the parents. Several such studies in passerines point at the adaptive hypothesis (Merkle and Barclay 1996; Slagsvold and Johansen 1998). Alternatively, energy expenditure and time budgets of parent birds could be compared between the incubation and chick-rearing periods, along the lines explored by Ashkenazie & Safriel (1979) and Maxson & Oring (1980), but employing more modern methods for measuring metabolism. Neither approach has yet been applied in birds with self-feeding chicks.

Body size and latitude

The breeding range of little stints extends almost continuously from northern Norway to the Chukotski Peninsula (Underhill et al., unpubl. data). No longitudinal cline in body size of little stints was found across the 8000 km range (Underhill et al., unpubl. data). This was attributed to the species' lack of breeding site fidelity (shown by Underhill et al. (1993) and Tomkovich & Soloviev (1994)), resulting in extensive gene flow. In the present analysis, we found an increase in body size with latitude. There are two possible explanations for this finding: either the sex ratio shows a latitudinal pattern, with more females incubating in the north, or larger individuals of both sexes breed in the most northerly areas. Among the sexed birds, no significant relationship between wing length and latitude was found within sexes, arguing against geographic variation. Sex ratios observed in our different study sites, combined with the available literature, suggest a skewed sex ratio (table 5.4).

A preponderance of females at high latitudes could result from the double-clutch breeding system found in this species, if females leave their first-laid clutch to be incubated by males and migrate further northward before producing a second clutch. Such a scenario has been indicated in the closely related, double-clutching, Temminck's stint *Calidris teminckii*. Hildén (1975) found some females immigrating and laying in his Finnish study area after most first clutches had been laid. At the same time other females, that had produced a first clutch (incubated by the male) locally, left the area. Because the study was conducted near the southern edge of the breeding range and emigrant females strongly outnumbered immigrants, Hildén (1975) inferred that females mainly moved northwards between clutches. Breiehagen (1989) recorded 61% females in a Norwegian study site with

a relatively late snow melt, the excess of females being largest in late-melting parts of the area, and suggested that female Temmick's stints follow the progress of snow-melt between the laying of successive clutches. Tomkovich (1988) similarly observed a late arrival and predominance of females in NW-Taimyr, near the northern edge of the species' breeding range.

A different explanation for the cline in sex ratios would be a latitudinal trend in mating system. If northerly breeding little stints were monogamous while southern birds adopt the double-clutching system, this could explain the larger proportion of females among birds incubating in the north, provided that females take the greater part of the incubation duties. However, there is no evidence for such geographical variation in mating system of little stints, and in monogamously breeding calidridine sandpipers, incubation duties are usually shared equally between the sexes or skewed towards the male (e.g. Borowik and McLennan 1999). Clearly, more data on the mating strategies and within-season movements of little stints throughout their breeding range are needed to elucidate this matter.

Latitudinal variation in energy stores

Geographic variation in midwinter body mass of waders wintering at different latitudes has been interpreted as a reflection of variation in the probability of encountering bad weather and periods during which feeding areas are not accessible (Pienkowski et al. 1979; Davidson 1981; Summers et al. 1989; Castro et al. 1992; Piersma et al. 1994; Zwarts et al. 1996). Although the latitudinal range over which little stints disperse in the breeding period is not as large as, for instance, that in the wintering range in dunlins or sanderlings (Cramp and Simmons 1983), a considerable gradient also in climatic conditions exists in the breeding range.

Over the six degree range in latitude covered by our dataset, mean body mass during incubation increased from 27.6 g at 70° N to 31.2 g at 76°N. Part of this increase is explained by the latitudinal trend in structural size as measured by wing length. However, after allowing for the wing length effect, there was still a significant increase in (residual) mass with latitude, and the same was found when mass was corrected for size using an independent measure of structural size (i.e. African winter mass predicted from wing length). Moreover, it was also present within each sex, while there was no increase in wing length with latitude within sexes. Hence, little stints incubating in northern sites had larger energy stores than those more to the south, and similar adaptations to the risk of encountering periods of energy imbalance as found in the wintering areas, also exist in the reproductive period.

Without knowing the composition of the energy stores, it is difficult to interpret their value in terms of survival time. However, based on doubly-labeled water estimates of field metabolic rate at Medusa Bay, where incubating little stints operate on average at 1.7 W (chapter 6), the 8 g of stores of birds at 76°N would suffice for 2.1 days if consisting entirely of fat (energy density 39 kJ/g), and 0.4 days if consisting of lean tissue only (7 kJ/g). After hatching, the stores decreased in size, but since most chick-rearing birds were weighed within the period of declining mass shortly after hatching, it is difficult to say to what level. Nevertheless, the observed masses already represent a loss of 31-38% of the stores present during incubation.

Conclusion

The climate data show that the risk that breeding little stints encounter cold weather lasting several days increases with latitude, and decreases from June to July. The observed geographical pattern of a higher body mass at more northerly breeding sites therefore agrees with the notion that the optimal size of avian energy stores increases with the risk of encountering periods of negative energy balance potentially leading to starvation. The loss of mass between incubation and chick periods also agrees with this notion, although the alternative explanation of a negative energy balance during chick-rearing cannot be excluded on the present data.

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Voorbereid op de kou

Kleine strandlopers hebben een bijzonder broedsysteem. Het vrouwtje legt vier eieren en laat het uitbroeden daarvan vervolgens aan het mannetje over. Zelf gaat ze op zoek naar een ander mannetje en legt nog een keer vier eieren, die ze dan zelf uitbroedt. Door dit systeem hebben ze tijdens het broeden weinig tijd om voedsel te zoeken: de eieren moeten immers warm gehouden worden. Dat is waarschijnlijk de reden waarom één van de kleinste steltlopers die in de Arctis broeden zo zwaar is in deze periode. Ze onderhouden een flinke reservevoorraad, zodat als het een tijd slecht weer is, ze toch de eieren kunnen blijven bebroeden. Tijdens het broeden zijn ze tot wel 1,5 keer zo zwaar als in de winter in Afrika.

Het broedgebied van kleine strandlopers is enorm groot: het strekt zich uit van Noord Scandinavië tot aan Oost Siberië. Naarmate je verder naar het noorden komt is de kans op slecht weer ook groter. Dat zie je ook terug in de gewichten van de kleine strandlopers tijdens het broeden. Door gegevens bij elkaar te brengen die op 12 verschillende plekken in de Arctis zijn verzameld hebben we ontdekt dat dieren die verder naar het noorden broeden zwaarder zijn. Dat wordt deels veroorzaakt doordat er in het noorden meer vrouwtjes zitten, die iets groter en dus zwaarder zijn dan mannetjes. Maar zelfs als je daarvoor corrigeert zijn de noordelijker vogels ook gewoon echt zwaarder. Het feit dat er in het noorden meer vrouwtjes zitten, doet ook vermoeden dat de vrouwtjes nadat ze het eerste legsel voltooid hebben nog een paar honderd kilometer verder noordwaarts vliegen voor dat ze (waarschijnlijk met een ander mannetje) een tweede legsel produceren. Op die manier zouden ze 'het seizoen kunnen inhalen' en zorgen dat ook het tweede legsel uitkomt op een moment dat er voldoende voedsel voor de kuikens beschikbaar is.

Opvallend is dat wanneer de kuikens er eenmaal zijn, het gewicht van de ouders heel snel afneemt. Dat zou kunnen komen omdat het zoveel energie kost om voor de kuikens te zorgen dat ze vanzelf afvallen, of misschien passen ze hun gewicht actief aan, omdat het dan niet meer nodig is als reserve. Het is dan inmiddels warmer weer met meer voedsel en ze hebben meer tijd om voedsel te zoeken.



Chapter 6



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Incubation and chick-rearing in high arctic breeding shorebirds: what is the most demanding phase?

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The timing of breeding significantly affects breeding success of birds, especially in strongly seasonal environments. Traditionally, rearing young is regarded as the energetically most demanding phase of the breeding cycle, but selection on breeding phenology may not only be tuned to maximise food availability for the young, but also to energetic requirements of parents.

Arctic breeding shorebirds face high energy expenditure during breeding. As they are too small to carry sufficient stores to sit out the incubation period, they regularly interrupt incubation to feed. As a consequence, they may become energy-stressed, particularly in species where one adult takes care of eggs and chicks alone. We measured daily energy expenditure (DEE) and time budgets during incubation and chick-rearing in the smallest uniparental arctic shorebird, little stint. DEE decreased with increasing temperature, but did not differ between the periods. DEE divided by potential foraging time determines the energy intake rate during foraging (RI) required to balance the budget. RI was lower during chick-rearing than incubation due to an increase in potential foraging time. Comparison of RI with arthropod abundance (a proxy for potential food intake rate) yields a measure of energetic stress. The greater food availability and foraging time during chick-rearing resulted in a reduced energetic stress. To evaluate the effect of uniparental care on energetic stress we also measured DEE in dunlin, a sympatric congener in which both parents incubate but the female deserts after hatching. DEE decreased with temperature, was equal during incubation and chick-rearing, and was higher in males. Because of reduced potential feeding time, RI was raised in males during chick-rearing compared to incubation. Despite higher food availability during chick-rearing, this period was equally stressful energetically as incubation. Our results can explain the relationship between timing of breeding and parental care system generally observed in arctic shorebirds. In uniparental incubators, energetic stress is higher during incubation, and energy requirements of the parents relative to those of the chicks are more important than in biparental species. For uniparental incubators this would result in a later optimal time of breeding, closer to the seasonal food peak.

Introduction

Generally, the period of feeding young is regarded as one of the energetically most demanding periods in the annual cycle of birds (Drent and Daan 1980; Weathers and Sullivan 1993). The high level of energy expenditure of parents with dependent offspring has long been regarded as a major evolutionary force shaping clutch size (Lack 1968; Drent and Daan 1980). In species that feed their young, numerous provisioning flights from the food source to the chicks result in higher energy expenditure compared with the incubation period (Bryant and Tatner 1991). However, in precocial species with self-feeding chicks like shorebirds, this period is likely to be less demanding for the parents, because they do not have to provision their young. Although shorebird chicks require vigilance from the adults, we predict that this entails no extra costs for the adults, since guarding of young can be combined with foraging for themselves. The decision of when to breed may not only be strongly shaped by the chicks needs, but also by energetic requirements of the parents during the incubation and chick-rearing phase (Perrins 1970; Drent 2006). This may be especially the case in strong seasonal environments that are often characterised by a short reproductive window, due to highly dynamic changes in weather and food conditions.

Although incubation has long been thought to be an energetically inexpensive activity in terms of energy expenditure, recent work has shown that incubation is costly (Tinbergen and Williams 2002; de Heij 2006), and especially so for arctic breeding birds (Piersma et al. 2003). A substantial proportion of the energetic cost of incubation occurs while rewarming a clutch that has cooled down, but foraging on the open, windswept arctic tundra is even more expensive than incubating in a sheltered nest-cup (Piersma et al. 2003; Cresswell et al. 2004). Especially in uniparental species, clutches are regularly left alone when the sole incubating parent goes off to feed (chapter 4), and cooling and rewarming of eggs occur frequently (Williams 1996). This pattern of intermittent incubation is likely to increase energy expenditure compared to an incubation pattern in which the optimal clutch temperature is maintained for prolonged periods (Tinbergen & Williams, 2002; Williams, 1996). Simultaneously, the time available for foraging is restricted by the need to incubate the clutch, and is generally more limited in uniparental incubators (13-19% of the day, Cartar and Montgomerie 1987, Norton 1972, chapter 4) than in biparental species (circa 50%, depending on the sex roles, Cresswell et al. 2003, Norton 1972). Time and energy budgets of biparental incubators (where both parents share incubation duties) are therefore likely to be less tight compared with those of uniparental species.

Whether the energetic demands during incubation or chick-rearing are merely demanding or energetically stressful depends on the possibilities for energy uptake. Energy expenditure may be high, but this does not necessarily have to be stressful if it is matched by a high energy uptake. Vice versa, a stressful situation may arise even at low energetic costs, if possibilities for energy uptake are limited. Food availability for arctic breeding shorebirds that feed on surface active arthropod prey is not constant over time, but shows a strong seasonality, with a superimposed effect of weather (chapter 9). The ratio between daily energy expenditure (DEE) and potential foraging time determines the intake rate during foraging required to balance the energy budget. The required energy intake for a day (kJ) divided by the foraging time window (s) gives us the required minimum energy intake during foraging. An indicator of relative energetic stress an animal is subjected to, allowing comparison between incubation and chick-rearing, can be calculated if the required intake rates (while feeding, IR_f) are combined with a measure of food availability.

The relative magnitude of energetic demand during the incubation compared to the chick-rearing period is likely to differ between fully precocial species and (semi-)altricials with parent-fed young. In addition, within each group it likely varies with the degree of sharing of incubation duties between the sexes. If precocial birds are more energy-stressed during incubation compared to the chick-rearing period, this should be most profound in a small species in a cold environment. We investigated how the incubation and chick-rearing phase compare energetically in the little stint *Calidris minuta*, one of the smallest representatives of uniparental precocial shorebirds breeding in the High Arctic. To explore the effect of parental role division on the relative energetic stress during the two breeding phases, we collected comparative data on the closely related dunlin *Calidris alpina*, a biparental species occurring in the same area.

Methods

Study area and species

Data were collected during June-early August of 1996 and 2000-2002 at Medusa Bay, on the Taimyr peninsula, Siberia (73°20'N 80°30'E). At this latitude there is continuous daylight throughout the breeding period. The habitat consists of arctic tundra (Chernov 1985), with a rolling relief between 0 and 50 m above sea level, and scattered stony ridges. Vegetation consisted of mosses, lichens and grasses generally not higher than 10 cm with a significant proportion of bare soil. Lower lying wet valleys were covered with sedges and low polar willow shrubs *Salix* spp. Little stint females produce two clutches of which the first is usually incubated by the male and the second by the female. Consequently, both parents take care of a clutch and brood alone (Hildén 1978; chapter 5). Nests of little stints are generally located in or close to grass or sedge fields, often in valleys or on south facing slopes. The nest cups are filled with a thick layer (mean 2.9 cm, SD = 1.5, N = 60) of dry willow leaves (chapter 3). In dunlin, male and female divide incubation duties equally, but females desert the brood after hatching (Crampton and Simmons 1983). Dunlin nests are found on the higher part of slopes and on flat ridge tops, in relatively dry, frost-boiled tundra. The nest cup lining consists of a 1-2 cm thick layer of willow leaves, lichen, sedge and grass (mean 1.8 cm, SD = 0.8, N = 22, chapter 3). Despite the differences in breeding habitat the two species often breed in close proximity.

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. In 2001 and 2002 all weather data, and in 1996 and 2000 air temperature, 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 height. Daily mean temperature varied between 0°C and 15°C and 0°C and 20°C in June and July, respectively. The amount of precipitation was generally low, apart from 2002, when total rainfall in June-August was 130 mm.

Catching birds

Nests were located by intensive searching during the laying and incubation periods. All nests of which the adults were subjected to energy expenditure measurements contained the set of four eggs characteristic for the species. Nesting birds were caught using small clap nets that were set up over the nest and released by the bird when it returned to the eggs. To avoid nest desertion, we only caught birds from the second week of incubation

onwards. Birds tending chicks were captured with the same clap net, or with a mist net that was held between two observers and pulled over the approaching bird. In both cases, the adult was lured to the net by placing the chicks in a small cage. Birds were usually caught within 10 min after the first disturbance. Captured birds were ringed with metal rings and individual colour ring combinations. Bill length was measured to the nearest 0.1 mm using callipers. Wing length (maximum chord, 1 mm) was measured with a stopped ruler. Pesola spring balances were used to measure body mass (to 0.1 g). Dunlins were sexed based on plumage characteristics and size (Prater et al. 1977). Little stints could not be reliably sexed based on external dimensions or plumage.

Doubly labelled water experiments

Measurements of DEE (kJ/day) were made in a variety of weather conditions, using the Doubly Labelled Water (DLW) method (Lifson and McClintock 1966; Speakman 1997). In addition to the 30 experiments made in this study, we also included three previously published measurements on incubating little stints collected at another site in Taimyr, Cape Sterlegov (75°25'N, 89°08'E, Piersma et al. 2003). For 23 of the 33 measurements in little stint and 12 of the 20 measurements in dunlin we followed a two-sample protocol with both an initial and a final measurement of isotope concentrations. For the remaining measurements we applied a single sample protocol (Webster and Weathers 1989) and took only a final blood sample to minimise capture and handling stress and thereby reduce the risk of nest desertion or brood disruption (see appendices 6.1 and 6.2).

All experimental birds were injected subcutaneously in the brood patch area with a known quantity (0.10-0.20 ml) of DLW consisting of 32% D₂O and 68% H₂¹⁸O. Birds subjected to the two-sample protocol were kept in a bag for an equilibration period of 1 hour, while their chicks were kept warm using a warm water bottle. Eggs were covered to slow down cooling. After one hour in which also biometrical measurements were taken, four to six blood samples (10-15 µl) were collected from the brachial vein in the wing into glass capillary tubes, which were flame-sealed within minutes. Adults and chicks were subsequently released together. Birds subjected to the single-sample protocol were released immediately after injection and biometric measurements. All birds were recaptured after 23-28 h in little stint (mean 24.5 h, SD = 1.1, N = 33) and after 23-32 h (mean 24.8 h, SD = 1.8, N = 18) or 48 h (SD = 0, N = 2) in dunlin, when a final set of blood samples and measurements were taken. Incubating birds were recaptured on the nest; chick-rearing birds were recaptured on or near their chicks after the brood had been relocated.

Initial isotope concentrations were measured directly in the initial blood samples taken in the two-sample protocol. For birds subjected to the single-sample protocol, initial concentrations were calculated from the amount injected and estimates of the size of the total body water pool. This estimation was based on a regression of initial isotope levels on body mass in birds in which a double sample protocol was carried out. In three adults of each species and in each year, a set of blood samples was taken before injection of DLW, to measure background isotope levels. The ratios ²H/¹H and ¹⁸O/¹⁶O in the blood samples were analysed with a SIRA 9 isotope ratio mass spectrometer at the Centre for isotope Research, Groningen, following procedures described in Visser and Schekkerman (1999). Analyses were done in duplicate and in triplicate if the two measurements differed by more than 2%. The percentage of body water was calculated with the isotope dilution method using the plateau values of the ²H₂¹⁸O enrichments above the average background concentrations and the dose. We calculated CO₂-production based on equation 7.17 in Speakman (1997).

DEE was calculated using an energy equivalent of 27.33 kJ/l CO₂ for a protein-rich diet (Gessaman and Nagy 1988). Metabolisable energy (ME) was calculated by adding energy deposited into new tissue to DEE in case the bird gained weight over the measurement period. ME was equal to DEE if no weight gain occurred. Energy density was estimated to be 39 kJ/g body mass (Ricklefs 1974) i.e. assuming that body mass variation involves mainly variation in fat stores.

Multiple regression analysis was used to investigate the relationship between DEE and explanatory variables. Mean temperature and wind speed were averaged over the period between injection and recapture for every doubly labelled water experiment and incorporated in the model together with wing length, body mass, time period relative to the date of hatching (days) and the breeding phase (incubation or chick-rearing). In dunlin, also effects of sex were tested.

Time budgets of little stint

Incubation schedules in the little stint were recorded from nest temperature measurements carried out with a small temperature probe (2 x 5 mm, temperature range -10°C to 50°C) positioned between the eggs and connected by a thin wire to a waterproof data logger (Tiny Tag, Gemini, chapter 4). 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 for over 11 days of temperature recording at one minute intervals. The loggers were covered with moss to avoid attracting predators. They were replaced after 11 days, or collected after the chicks had hatched or the nest was depredated. Start and end of incubation recesses were determined from graphs of temperature in relation to time. For further description of data handling see (chapter 4).

Time budgets of little stints tending chicks were collected by visual observation, using a telescope from a slightly elevated observation point. Little stint families with young chicks generally prefer short vegetation on low-lying sedge fields. Families can be approached at close range and will show apparently undisturbed behaviour at short distances (20-50 m in young broods and 100 m in older broods). Duration of brooding and non-brooding bouts and the activity of the parent and chicks were registered. This was used to obtain age- and temperature-specific estimates of brooding and foraging time. Broods formed the statistical unit, as the alteration between brooding and feeding is highly synchronized among chicks of one brood. Brooding and non-brooding bouts were timed to the nearest 10 sec, and the total time minus the time spent brooding (the recess time) constitutes the 'potential foraging time' for the adult. Actual foraging time was determined by estimating the proportion of the duration of non-breeding bouts that the parent spent foraging as opposed to other behaviours. Due to the sometimes rapid alternation between feeding and vigilance/communicating with chicks, this estimate has a limited precision of 10-20%. Chicks were weighed every two days.

Observations were made on six different broods in 2000, 2001 and 2002. Observation periods (N = 40) were scattered throughout the 24 hours of daylight and at all stages of chick development, from hatching to 17 days after hatching, and totalled 60.9 hours in bouts of 38-130 minutes (mean 91, SD = 25 minutes). Observation sessions started in all of the 24 clock-hours except between 22:00 and 02:00 h. Multiple regression was used to investigate the relation between total observation time spent brooding in relation to age, temperature and time (e.g. whether it was 'day' (between 04:00 and 22:00 h, when light levels and tem-

peratures are generally highest) or 'night' (between 22:00 and 04:00 h). Proportions were logit-transformed before analysis.

However, observations on time budgets of dunlin families were not possible due to their poor visibility in generally higher and denser vegetation, combined with more wary parents and inconspicuous behaviour of the chicks. For the incubating period we rely on time budgets published in the literature (Norton 1972; Cresswell et al. 2003). To compare time-energy budgets between species, we assumed the time budget of chick-rearing dunlin to be similar to that of little stint.

Energy expenditure, time budgets and food availability

Required intake rate was calculated as the minimum intake rate needed to balance energy intake with ME on a daily basis. In order to standardize values, we first calculated the mean temperature during the incubation period (range between start of the first and the last nest) and chick-rearing period (range between hatching of the first and the last nest) for little stint and dunlin separately for every year in 2000-2002 (Schekkerman et al. 2004). Values for temperature and food availability for 1996 were excluded from this analysis, as in this year the fieldwork did cover the whole incubation period, but only the start of the chick-rearing period. The mean of the values per year were used as input for the following calculations. Based on the relationships between DEE (ME) and temperature (this study) and between available foraging time and temperature during incubation (derived from chapter 4) and during chick-rearing (this study), we estimated the required metabolisable intake rate while feeding: $IR_f = ME / \text{foraging time}$. These intake rate requirements are 'net' or 'metabolisable' intake rates (i.e. the product of gross intake rate, digestive efficiency and assimilation efficiency). For dunlin during chick-rearing the same actual foraging time was used as in little stints. Based on the assumption that food intake rate is affected by food abundance, we used the daily abundance of arthropod prey as measured by pitfall trapping (chapter 9) as an estimator for potential intake rate. Mean arthropod abundance was calculated for the incubation and chick-rearing period in the three years separately and averaged. An index of the relative energetic stress experienced by the birds was calculated by dividing the required intake rate while feeding by arthropod abundance. An absolute measure of stress levels can only be calculated if the functional response (relationship between arthropod abundance and intake rate) is known, which was not the case in this study.

Results

Daily energy expenditure in little stint

DEE in little stint was negatively correlated with mean temperature over the period of measurement ($F_{1,31} = 4.7$, $p = 0.038$, figure 6.1). In a regression analysing both phases simultaneously, body mass, wing length, days to hatching, mass change and breeding phase had no significant effect on DEE (all $p > 0.05$). The interaction term between phase and temperature was not significant, indicating that the slope for the relation between DEE and mean temperature did not differ between the two phases. On average, DEE in little stints was 156.3 kJ/day (both phases combined, see appendix 6.1).

Time budget of little stint

During incubation, little stints spent on average 18.8% (SD 7.7%, 4.4 hrs) of the day ($N = 197$) away from the nest with no variation caused by the stage of incubation (chapter 4). Total

Figure 6.1. Daily energy expenditure in incubating and chick-rearing little stints as a function of the mean temperature over the measurement period. The three points collected at a different site (Cape Sterlegov) are indicated with a different symbol. The line represents the overall significant regression line for DEE as a function of temperature. After correction for temperature there was no difference in DEE between incubating and chick rearing little stints.

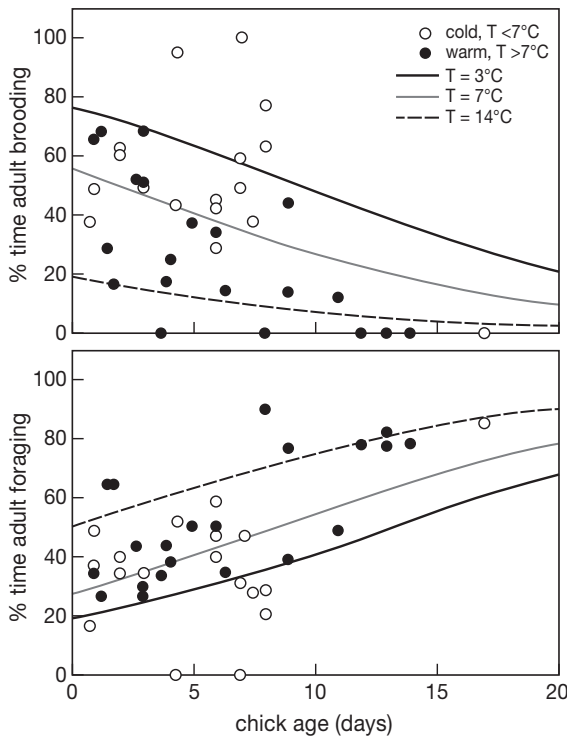
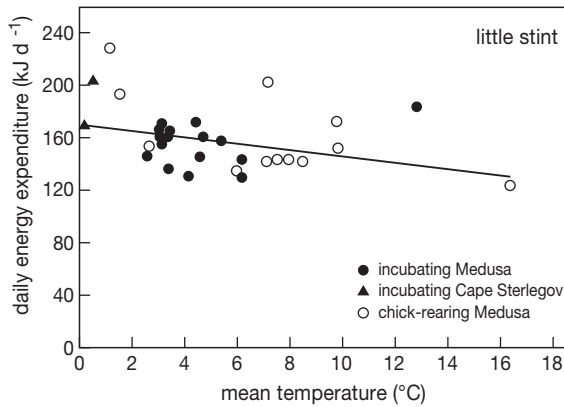


Figure 6.2. Percentage of time spent brooding (left) and foraging (right) little stints in relation to age (days) and air temperature. The fitted lines are the outcome of a logistic regression for the lowest (3°C), mean (7°C) and highest (14°C) air temperatures during observations.

recess time decreased slightly with increasing temperature from 5 hours/day at 0°C to on average 4 hours/day at 14°C (chapter 4). Occasional observations of birds during incubation recesses suggest that they use virtually all of this time for foraging, exhibiting noticeably more hasty movements than prior to breeding.

During the chick rearing phase, time spent foraging increased significantly with chick age and temperature (table 6.1, figure 6.2). Parents with chicks up to one week old spent on average 46.1% (SD = 22.6, N = 28) of the time brooding and 37.3% foraging (SD = 15.6, N = 28). Parents tending older chicks spent 20.5% (SD = 27.7, N = 12) of their time brooding and 60.7% foraging (SD = 25.9, N = 12). Other activities, including preening, walking and vigilance, were observed for 17% (SD = 17.1) of the time during the first week and 20% thereafter (SD = 10.9). In addition, there was a tendency for brooding time to be increased between 22:00 and 04:00 hours, indicative of a circadian activity rhythm with sleep accommodated into night-time brooding bouts, but this was not significant ($P = 0.18$), possibly as a consequence of the small sample size for “night” relative to “day”. Interactions between age, temperature and “night” were not significant (all $P > 0.05$), nor were additional effects of wind ($P = 0.36$), or rainfall ($P = 0.22$), in a model containing age and temperature. Results of both analyses were very similar if body mass of the chicks was used as a predictor of brooding time instead of their age.

Time-energy budget of little stints during incubation and chick-rearing

Based on the relationship between total recess time and mean temperature from chapter 4, incubating little stints spend on average 4.4 hrs per day feeding at a mean temperature of 3.3°C. In the chick-rearing period, parents with five-day old chicks spend an estimated 9.7 hours per day on foraging (at a mean temperature of 7.0°C). The required net intake rate

Table 6.1. Multiple regression analysis for brooding and feeding time of adult little stint during incubation in 2000-2002 at Medusa Bay. F-probabilities are for terms sequentially added to the model; estimates (logit proportion of time brooded) are for the final model including all variables).

variable added	df	SS	variance ratio	F-probability	estimate (logit)	SE
% feeding time						
constant					-1.872	0.345
age	1	0.5734	22.70	<0.001	0.1120	0.0308
temperature	1	0.3117	12.34	0.001	0.1333	0.0395
residual	37	0.9688				
total		1.8539				
% of time brooding						
constant					1.8830	0.4930
age	1	0.6628	18.14	<0.001	-0.1247	0.0470
temperature	1	0.7306	20.00	<0.001	-0.2349	0.0622
residual	37	1.3830				
total		2.7760				

Table 6.2a. Overview of the mean temperature (average value over the years 2000-2002), DEE (J/s), ME (DEE taking mass changes into account), available foraging time throughout the day, the required intake rate during foraging to balance mass loss and the available arthropod food for little stint. Values are given for the two phases of the breeding period (incubation and chick rearing). DEE, ME, available foraging time and required metabolisable intake rate are all temperature dependent and values presented are for the mean temperature during the phase.

	incubation		chick-rearing (with five-day old chicks)	
	mean	SE	mean	SE
mean temperature	3.25	1.10	6.99	1.01
DEE (J/s)	1.87	0.05	1.76	0.05
ME corrected for mass loss (J/s)	1.87	0.06	1.74	0.05
available foraging time observed (hr/day)	4.38	0.19	9.74	3.94
required metabolisable intake rate (J/s)	10.22	0.54	4.28	1.73
available arthropod food (g dry mass/trap/day)	3.76	1.02	9.19	2.61

Table 6.2b. Overview of the mean temperature (average value over the years 2000-2002), DEE (J/s), ME (DEE taking mass changes into account), available foraging time throughout the day, the required intake rate during foraging to balance mass loss and the available arthropod food for dunlin. Values are given for the two phases of the breeding period (incubation and chick rearing). DEE, ME, available foraging time and required metabolisable intake rate are all temperature dependent and values presented are for the mean temperature during the phase. Data are given for males and females separately.

	incubation				chick-rearing (males) (with five-day old chicks)			
	males		females					
	mean	SE	mean	SE	mean	SE	mean	SE
mean temperature	2.83	1.34	2.83	1.34	6.49	1.67		
DEE (J/s)	3.03	0.25	2.52	0.26	2.83	0.25		
ME corrected for mass loss (J/s)	2.60	0.40	2.57	0.41	2.77	0.39		
available foraging time observed (hr/day)	12.00	0.00	12.00	0.00	9.36	3.94		
required metabolisable intake rate (J/s)	5.20	0.79	5.04	0.53	7.94	3.41		
available arthropod food (g dry mass/trap/day)	3.13	1.12	3.13	1.12	8.14	1.12		

while foraging is 10.2 J/s in the incubation period (table 6.2a). In the chick phase this drops to 4.3 J/s because of much longer potential feeding time. Food availability increased from 3.8 to 9.2 mg dry mass/trap/day during incubation during chick-rearing (table 6.2a). The stress index decreased significantly between the phases (from 2.7 to 0.5, $Z = 2.86$, $P = 0.002$, figure 6.3).

Dunlin

DEE was on average 231.4 kJ/day and was not affected by body mass, wing length, days to hatching, mass change and phase. DEE was negatively related to mean temperature ($F_{1,19} = 10.65$, $P = 0.005$) and differed between the sexes (figure 6.4). Males had a significantly higher DEE than females ($F_{1,19} = 22.0$, $P < 0.001$). Adding sex to the model before mean temperature gave the same result.

Nest attendance as reported in the literature is more than 97% in dunlin, irrespective of weather (Norton 1972) and there is no indication that incubation duties are divided unequally between the sexes (Norton 1972; Cresswell et al. 2003). Therefore parents are off-duty on average 12 hours per day in the incubation period (given the continuous daylight). After hatching, potential foraging time for the male is reduced by the time needed to brood the chicks, since the female deserts the brood when chicks hatch or shortly after. We assumed the time budget of chick-rearing dunlin to be similar to that of little stint. This will slightly overestimate brooding times for parents of older chicks, because the larger dunlin chicks probably become homeothermic at an earlier age than little stints (at ca 10 days). Required intake rate during incubation (at a mean temperature of 2.8°C) is estimated at 5.2 and 5.0 J/s for males and females respectively during incubation and increases to 7.9 J/s for males tending five-day old chicks (at 6.5°C, table 6.2b). Due to the increase in temperature, food availability increased from 3.1 dry mass/trap/day during incubation to 8.1 mg in the chick period. The index for energetic stress decreased from 1.6 (males) and 1.7 (females) during incubation to 1.0 (males, figure 6.3), but this difference was not significant (males only: $Z = 0.88$, $P = 0.18$).

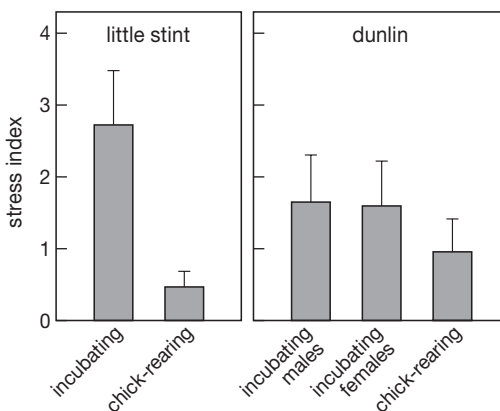


Figure 6.3. Index for stress (mean and SE) during incubation and chick-rearing for little stint (left) and dunlin (right). The difference between the phases was significant for little stint, but not for dunlin. The index was calculated as the required metabolisable intake rate at the mean temperature during incubation and chick-rearing (see tables 6.2a and 6.2b) divided by a measure of food availability (mean dry mass arthropods per pitfall trap per day). See text for further explanation on calculations.

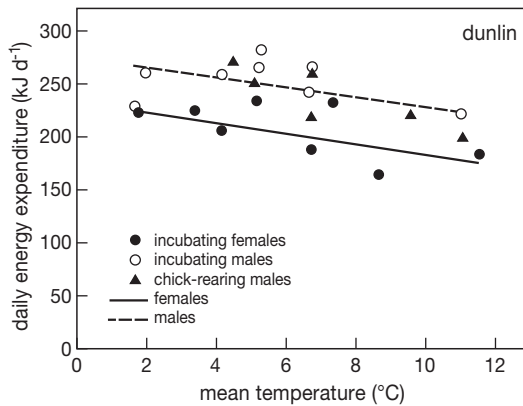


Figure 6.4. Daily energy expenditure in incubating and chick-rearing dunlin in relation to mean temperature. The lines represent the significant difference in DEE between males (dotted line) and females (solid line). There is no significant difference in DEE between incubation and chick rearing.

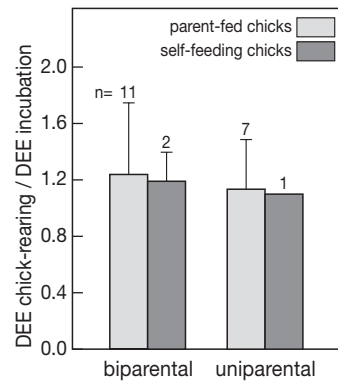


Figure 6.5. Ratio between DEE during chick-rearing and during incubation in biparental and uniparental self-feeding and parent-fed species. Data from (Tinbergen and Williams 2002) updated with little stint and dunlin (this study). Error bars represent 95% confidence intervals.

Discussion

DEE in arctic breeding shorebirds

Based on the allometric relation between DEE and body mass in incubating and chick-rearing birds derived by Tatner and Bryant (1993), DEE is predicted to be 99.5 kJ/day for incubating and 118.9 kJ/day for chick-rearing little stints. For dunlin these predictions are 164.3 kJ/day and 134.3 kJ/day respectively. The measured values exceed the allometric predictions by 34-55% (little stint) and 39-77% (dunlin). However, this predictive equation is based on temperate breeding birds only, and mainly on passerines. The higher DEE measured in this study is consistent with the finding that DEE is about 50% higher in birds breeding in the Arctic than at temperate latitudes (Tinbergen and Williams 2002). Compared with the regression equation relating DEE to body mass for arctic breeding shorebirds (Piersma et al. 2003) our value for little stint is 9% lower (149.2 kJ/day, excluding the three Cape Sterlegov points which were included in the allometric prediction, vs a predicted 164.8 kJ/day). The value for dunlin fits very well (2% higher) with the regression equation. The lower value for little stint is likely caused by the difference in ambient temperature associated with nearly two degrees latitudinal difference between the study sites (see also figure 6.1). The study by Piersma et al. (2003) could not account for variation in temperature during the DEE experiments. Temperature was the most important variable explaining intraspecific variation in DEE in our study (see also Reid et al. 2000). A similar effect of temperature was found in a study on altitudinal variation in DEE in mountain breeding white-crowned sparrows *Zonotrichia leucophrys* (Weathers et al. 2002).

DEE in dunlin

In dunlin, DEE was significantly larger in males than in females (figure 6.4), despite the males' smaller size. This difference might reflect the extra costs associated with aerial and song display that males perform during the incubation period. Territorial behaviour is less prominent after hatching (Cramp and Simmons 1983), but whether the intensity of these displays remains constant or is reduced during incubation is not known. An alternative explanation might be that dunlin males may have a more intense moult during incubation than females. Both male and female start moulting their primaries already early in incubation and finish close to departure in autumn (Kania 1990; Tulp and Schekkerman 2001). However, there was no effect of sex on the development of primary moult score in data collected in our study area (logistic regression, date: $p < 0.001$, sex: NS, $N = 36$ females, 46 males). Furthermore, an unequal division of incubation shifts over day and night between the sexes could lead to a higher DEE in males if males incubate mainly during the day. Their off-duty period would then be in the coldest part of the day, with lower temperatures and therefore higher energy expenditure during their feeding recess. Such unequal division with males incubating predominantly during the day has been demonstrated in the Baltic Sea area (Heldt 1966; Soikkeli 1974), but it has not been investigated in the Siberian Arctic. Based on what sexes were present at the times of catching, there was no indication of an unequal division of day and night shifts between the sexes in our study. In a total of 76 catches the proportion of males in the catches done before 18:00 ($N = 48$) was 60%, compared with 50% after 18:00 (total $N = 28$). Alternatively, our assumption that incubation shifts are equally long in both sexes as found in Alaska (Norton 1972; Cresswell et al. 2003), might not be applicable to Taimyr dunlin.

DEE unrelated to phase of breeding

DEE did not differ between the incubation and chick-rearing periods in either species. There are several explanations for this. In the Arctic, weather conditions are generally more benign during the chick-rearing period (Schekkerman et al. 2004). Mean temperature during incubation over the three years was 3.3°C and 2.8°C for little stint and dunlin, respectively. During chick-rearing mean temperature was 7.0°C and 6.5°C (tables 6.2a and 6.2b). As we used actual measurements of DEE and did not standardize them to a fixed temperature, the general increase in temperature (and therefore reduction in thermoregulatory costs) that takes place in most years from June (when most birds are on the nest) to July (when chicks hatch) is incorporated in the phase comparisons. Another explanation might be that activity costs are relatively high during chick-rearing as compared to incubation.

In a study in which DEE during incubation was compared with that during chick-rearing (Tatner and Bryant 1993), differences between the two stages were found in only five out of 16 bird species. In these species, all of which do feed their (artificial and semiprecocial) chicks, DEE was larger during brood-rearing. In the single shorebird in this study, the biparental common sandpiper *Actitis hypoleucos*, no difference was found. Williams (1996) analysed DEE during the two stages for uniparentals and biparentals separately and found no difference between the two phases in either group. However, the ratio of DEE during chick-rearing to DEE during incubation was significantly lower in uniparental than in biparental species, suggesting that the single parent has to work relatively harder in the incubation phase compared with biparental species.

Combining the set of Tatner and Bryant (1993), updated by Tinbergen and Williams (2002) with our data, the average ratio between DEE in the two phases for adults with self-

feeding chicks (little stint, dunlin and common sandpiper) is identical (mean = 1.20, SD = 0.23, N = 3) to the ratio for adults that provision their young (mean = 1.16, SD = 0.09, N = 18). Although not significantly this ratio tends to decrease in the order: 1. biparental species with parent-fed chicks, 2. biparental species with self-feeding chicks, 3. uniparental species with parent-fed chicks to 4. uniparental species with self-feeding-chicks (figure 6.5).

When do energetic demands cause stress?

The combination of time and energy budgets identifies the incubation phase as the most energetically demanding for uniparental little stint, while for dunlin single-handed chick-rearing is more demanding than biparental incubation in terms of the required intake rate. Using food availability as a proxy for potential energy intake rate during feeding, the resulting index for stress is much larger during incubation than during chick-rearing in little stint, while for dunlin there is no significant difference. This pattern arose primarily from differences in the foraging time window, rather than from differences in energy expenditure. Our index for energetic stress does not quantify in absolute terms when an energetically stressful situation arises, and we don't know the functional response for arctic breeding shorebirds feeding on arthropods. However, the index used is closer to absolute stress than required intake rate alone would be, and hence is useful in a comparative sense.

The idea that incubation is energetically more demanding and at times stressful for uniparental incubators is corroborated by body mass dynamics in our two study species. Arctic shorebirds generally maintain higher body mass during incubation than during chick-rearing and there are indications that the sudden drop in body mass frequently observed at hatching is a preparation for the period in which adults must guard the chicks, rather than the outcome of increased energetic stress (chapter 5). A gradual decrease in body mass in the course of the incubation period was not observed in either species. This indicates that under normal conditions DEE is not fuelled from energy stores accumulated before breeding (i.e. they are 'income' breeders and not 'capital' breeders, Klaassen et al. 2001). However, little stints do show a decrease in body mass in response to several consecutive days of adverse weather (chapter 4). Apparently the energy budget cannot be balanced in such periods, because the required intake rate cannot be achieved as a result of reduced food availability, elevated energy expenditure and reduced feeding time. The lack of a similar response to weather in dunlin (chapter 4), strengthens the idea that for biparental incuba-



tors feeding time during incubation is less limiting. Another indication that energetic stress during incubation can be high for uniparentals is provided by the finding that nest desertion is more frequent in the uniparental little stint. In the period 2000-2002, only 1 out of 91 dunlin nests was deserted, but 19 out of the 331 little stints nests were ($\chi^2 = 3.41$, $P = 0.06$, Schekkerman *et al.* 2004).

Energetic bottlenecks in relation to timing of breeding and parental care system

On the scale from uniparental to biparental, the dunlin does not represent a strictly biparental species. Both parents incubate the clutch, but chick-rearing is done by the males only. This system of parental care occurs in several arctic breeding calidrine sandpipers e.g. red knot *Calidris canutus* and purple sandpiper *C. maritima*, (Cramp and Simmons 1983). When chick-rearing duties are also shared between the parents, as in strict biparental species like many plovers, this period will be relatively less demanding due to the longer potential foraging time.

In comparison with birds that feed their young, chick-rearing is energetically less demanding than incubation in birds with self-feeding chicks. In altricial birds, parents have to make numerous trips to provide food for the young. Especially in altricials with uniparental care, the parent must be able to increase foraging efficiency to balance their own energy budget in the nestling period, otherwise lose mass. During incubation excess time not spent warming the clutch can be used for foraging. In the chick-rearing phase however, available feeding time has to be divided between the needs of the parent and those of the young. Very few studies exist that make a comparison in intake rates between these phases. In great tits *Parus major* females with nestlings deliver the same amount of food to the nestlings that they otherwise need for themselves (Tinbergen and Williams 2002). Due to the lower nest attendance in the nestling phase, the foraging intake rate during incubation is estimated to be 100% higher than for females that receive no assistance from their mate, but intake rates are similar between the incubation and nestling phase for birds that share incubation (Tinbergen and Williams 2002). Custer *et al.* (1986) measured energy budgets and intake rates in Lapland longspurs *Calcarius lapponicus*, an arctic passerine in which the female incubates and both parents feed the chicks. In this species DEE in both sexes was rather similar between the phases, but the maximum required intake rate per unit time foraging occurred in the nestling phase for both males and females.



The timing of breeding in birds often coincides with the seasonal maximum in the availability of food for chicks (Lack 1950), but may additionally be shaped by nutritional stress early in the egg-laying period (Perrins 1970), the minimization of energetic demands of parents during either incubation or chick-rearing, or even by future reproductive potential (Brinkhof et al. 2002; Hanssen et al. 2005). Because of the differences in time-energy budgets between uniparental and biparental species, food availability during incubation and chick-rearing may be an important factor determining the onset of reproduction. Early breeding is generally favourable for the chicks, because hatching then coincides with the peak in food supply. However, especially for uniparental incubators, food availability during incubation might constrain early breeding (Drent 2006). In our study area little stint start breeding later than dunlin (median first egg laying dates in 2000-2002, little stint: 18, 16 and 21 July, dunlin: 11, 8, 16 July respectively, Schekkerman et al. 2004). In general, shore-bird species with uniparental incubation tend to breed later than biparental incubators (Whitfield and Tomkovich 1996). Therefore a variety of optimality rules with respect to timing of breeding may apply for species that show different breeding strategies. Parental care systems thus impact optimal timing of breeding through energy balance in the different stages of breeding.

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Appendix 6.1. Daily energy expenditure of little stints during the incubation and chick-rearing phase as measured using the doubly labelled water method. Negative days to hatching means days prior to hatching, positive values represent age of chicks. #01,04,10 were collected at a different site at Cape Sterlegov in 1994 (Piersma et al. 2003). TBW=Total Body Water. Birds for which 'no initial' is mentioned under TBW were subjected to the single-sample protocol.

ID	wing length (mm)	start of experiment	N chicks	duration (h)	days to hatching/ age chicks (days)	mean body mass (g)	mean temp (°C)	DEE (kJ/day)	TBW (%)
incubating									
FS08202	97	26-Jun-96		23.9	-15	28.4	4.6	144.3	no initial
FS08205	99	24-Jun-96		23.9	-19	24.7	3.5	164.2	no initial
FS08207	94	26-Jun-96		24.5	-13	27.9	4.6	145.2	67.9
FS08209	95	27-Jun-96		23.9	-16	32.0	4.8	159.0	60.8
FS08210	95	29-Jun-96		24.4	-13	27.7	2.6	145.2	66.8
FS08215	97	04-Jul-96		24.8	-10	28.3	3.2	154.7	63.0
FS08218	97	03-Jul-96		25.5	-15	27.0	3.1	159.0	no initial
FS08220	96	06-Jul-96		28.1	-8	29.9	3.4	134.8	no initial
FS08224	98	30-Jun-96		24.4	-14	29.2	5.4	156.4	no initial
FS08231	98	03-Jul-96		25.4	-17	26.4	3.1	165.0	no initial
FS08232	99	05-Jul-96		24.1	-16	27.1	4.2	129.6	70.0
FS08233	100	05-Jul-96		24.9	-17	28.1	4.2	129.6	no initial
FS08251	100	06-Jul-96		25.3	-18	31.8	3.4	159.0	no initial
FS08256	101	08-Jul-96		23.8	-9	31.0	6.2	141.7	57.5
FS08257	102	08-Jul-96		24.0	-17	27.7	6.2	127.9	69.4
FS08258	95	08-Jul-96		24.2	-6	30.9	6.2	129.6	no initial
FS08259	100	09-Jul-96		25.1	-1	27.8	4.5	171.1	no initial
FS10710	97	29-Jun-01		24.8	-14	25.7	3.2	169.9	65.4
#01	102	09-Jul-94		21.4	?	30.2	12.9	181.8	63.3
#04	96	16-Jul-94		24.2	-11	29.0	0.6	203.1	72.2
#10	104	26-Jul-94		22.9	-1	28.8	0.3	169.4	71.9
average (SE)								154.3 (4.2)	66 (1.0)
chick-rearing									
FS10037	95	13-Jul-00	4	24.7	1	24.8	1.2	227.2	71.3
FS10033	97	19-Jul-00	4	23.3	3	27.4	1.58	193.2	65.2
FS10088	95	20-Jul-00	3	24.1	1	22.1	2.71	152.8	75.7
FS10089	102	22-Jul-00	4	24.6	1	31.2	8.5	140.5	65.2
FS10039	99	25-Jul-00	4	26.5	7	31.1	9.86	170.8	64.0
FS10047	101	25-Jul-00	4	24.6	6	27.1	9.81	151.6	68.1
FS10050	98	27-Jul-00	4	24.8	1	27.0	6	134.2	63.2
FS10096	98	28-Jul-00	4	25.1	4	27.7	7.99	142.1	66.4
KS06151	101	30-Jul-00	3	24.4	2	28.7	7.21	201.6	66.8
KS06153	104	30-Jul-00	4	23.9	2	28.2	7.17	140.2	64.1
KS06152	102	31-Jul-00	4	24.8	5	27.6	7.6	142.8	68.8
KS06246	102	01-Aug-00	2	24.7	5	30.7	16.43	121.5	63.5
average (SE)								159.9 (9.2)	66.9 (1.1)
overall average (SE)								156.3 (4.2)	66.5 (0.7)

Appendix 6.2. Daily energy expenditure of dunlin during the incubation and chick-rearing phase as measured using the doubly labelled water method. Negative days to hatching mean days prior to hatching, positive values in fact represent age of chicks. TBW=Total Body Water. Birds for which 'no initial' is mentioned under TBW were subjected to the single-sample protocol.

ID	sex	age	wing length (mm)	start of experiment	N chicks	duration (h)	days to hatching/ age chicks (days)	mean body mass (g)	mean temp (°C)	DEE (kJ/day)	TBW (%)
incubating											
KS06326	F	>2	120	03-Jul-02		24	-2	51.5	8.66	162.3	68.0
KS06353	M	>2	119	05-Jul-02		24	-3	51.0	1.97	258.1	66.6
KS06354	F	>2	121	06-Jul-02		32	-6	54.3	1.81	221.6	no initial
KS07204	M	2	114	07-Jul-02		25	-1	52.1	6.67	241.4	64.8
KS06355	F	>2	125	07-Jul-02		23	-3	56.3	7.37	230.9	68.9
KS06358	F	>2	121	08-Jul-02		24	-2	54.8	3.39	223.7	59.9
KS06363	M	2	115	10-Jul-02		23	-3	46.4	1.68	227.6	68.9
KS06364	M	>2	119	11-Jul-02		25	-3	54.7	5.21	264.4	no initial
KS06365	M	2	119	11-Jul-02		25	-11	49.5	5.34	279.9	no initial
KS07235	F	>2	118	01-Jul-01		25	-12	59.2	4.2	203.3	61.6
KS07236	M	>2	118	01-Jul-01		24	-10	54.0	4.2	256.7	67.3
KS07242	F	>2	116	06-Jul-01		25	-9	52.6	11.6	182.2	68.7
KS06106	F	>2	122	08-Jul-01		25	-9	52.9	6.8	185.4	no initial
KS07236	M	>2	118	08-Jul-01		48	-5	51.4	6.8	264.5	no initial
average (SE)										228.7 (9.4)	66.1 (0.9)
chick-rearing											
KS07237	M	>2	117	06-Jul-01	4	48	0	51.5	11.1	199.7	65.6
KS07446	M	>2	117	08-Jul-01	4	25	3	50.8	6.8	220.3	no initial
KS06204	M	2	114	17-Jul-01	4	24	1	44.3	6.8	260.1	71.1
KS07454	M	>2	116	18-Jul-01	3	25	3	46.8	5.1	251.1	no initial
KS07459	M	>2	116	19-Jul-01	4	25	2	47.5	4.5	272.3	no initial
KS07471	M	>1	114	23-Jul-01	3	25	3	42.5	9.6	222.3	70.9
average (SE)										237.6 (11.3)	69.2 (1.3)
overall average (SE)										231.4 (7.3)	66.9 (0.8)

De energiehuishouding van één- en tweoudergezinnen

Vergeleken met zangvogels hebben steltloperouders het relatief gemakkelijk. Als echte nestvlieders stappen de kuikens vanaf de eerste dag meteen rond en zoeken ze hun eigen voedsel. Omdat ze in de eerste week van hun leven hun eigen lichaamstemperatuur nog niet op peil kunnen houden, zoeken ze wel geregeld even hun ouders op om onder hun vleugels weer op te warmen. De rol van de ouders is dus wel een stuk eenvoudiger dan bij de nestblijvers, waar de jongen nog enkele weken in het nest blijven en gevoerd moeten worden. Ontelbare vluchten zijn nodig om de hongerige jongen te voeren. Steltloperouders kunnen terwijl ze met hun jongen over de toendra lopen gewoon ook zelf voedsel zoeken en hun rol blijft beperkt tot waken over de veiligheid van hun kroost en het af en toe opwarmen van verkleumde kuikens.

Op de toendra komen veel verschillende steltlopersoorten voor en de manier waarop ze hun gezinsleven organiseren verschilt nogal. Er zijn soorten waarbij de bijdrage van het mannetje beperkt blijft tot de bevruchting van de eieren, zoals de kempfaan, of waarbij het vrouwtje alleen de eieren legt, maar er vervolgens vandoor gaat, zoals bij franjepoten. Bij andere soorten wordt de ouderlijke zorg eerlijk verdeeld en zorgen beide ouders voor de eieren en kuikens. Dat systeem komt bij veel plevieren voor. En dan zijn er nog soorten die wel samen de eieren uitbroeden, maar waarbij het vrouwtje vertrekt zo gauw ze uitkomen. Het opvoeden van de kuikens wordt helemaal overgelaten aan de vader. Dit in het dierenrijk wat ongebruikelijke systeem komt onder andere voor bij de bonte strandloper en de kanoet. Vanuit het oogpunt van de energiehuishouding maakt het nogal wat uit of je er als ouder alleen voor staat, of dat je partner de helft van de tijd de eieren bebroedt, waardoor jezelf ruimschoots de tijd hebt om voedsel te zoeken. Soorten die alleen broeden, zoals de kleine strandloper en krombekstrandloper, zijn zo genoodzaakt van tijd tot tijd de eieren alleen te laten om voor zichzelf te foerageren.

Nieuwsgierig naar hoe de energiehuishouding wordt beïnvloed door het broedsysteem, hebben we de energie-uitgaven gemeten van kleine strandlopers en bonte strandlopers in de tijd dat ze hun eieren bebroeden en in de tijd dat ze met hun kuikens rondlopen. Dat kan je doen met behulp van de 'zwaar water methode', een methode waarbij je een klein druppeltje water inspuut dat naast normale water- en

zuurstofatomen, ook gelabelde, zwaardere, water- en zuurstofatomen bevat. Als aan een vogel een dosis van dit 'zware water' wordt toegediend, vermengt zich dat zeer snel met het lichaamsvocht. Daarna verdwijnen zowel de waterstof- als de zuurstof-isotopen weer langzaam uit het lichaam via urine, waterdamp in adem en zweet; het zuurstofisotoop verlaat het lichaam daarnaast ook nog in koolstofdioxidegas bij de uitademing. Het verschil in de snelheid waarmee de waterstof- en zuurstofisotopen worden uitgestoten is dus een maat voor de hoeveelheid koolstofdioxide die het dier geproduceerd heeft gedurende de meetperiode. En dat is op zijn beurt weer een maat voor het energieverbruik. Door vogels te vangen en met zwaar water in te spuiten, vlak daarna en opnieuw een dag later (na terugvangst van de vogel) een klein bloedmonster te verzamelen, kan uit het verschil in de isotopenconcentraties het energieverbruik worden berekend.

Vergeleken met soorten die in gematigde gebieden broeden, zijn arctische soorten meer energie kwijt tijdens het bebroeden van de eieren, gemiddeld zelfs zo'n 50% meer. Wat het broeden met name zo duur maakt, is niet zozeer het warm houden van de eieren, maar de foerageertochtjes tussendoor. Bovendien zijn de energie-uitgaven sterk weersafhankelijk: hoe kouder het wordt, hoe hoger het verbruik. Voor kleine strandlopers was er geen verschil in de dagelijkse energie-uitgaven tussen de incubatieperiode en de kuikenperiode. Hoe zwaar een dier het heeft hangt natuurlijk niet alleen af van de energie-uitgaven. Als er ruimschoots voldoende voedsel is en er is genoeg tijd om er naar te zoeken hoeft een hoge energiebehoefte nog geen stress op te leveren. Daarom hebben we ook gemeten hoeveel tijd kleine strandlopers hebben om voedsel te zoeken en hoeveel voedsel er is. Als de kuikens zijn geboren hebben ze tweemaal zoveel tijd om te foerageren (bijna 10 uur per dag) als tijdens het uitbroeden van de eieren (4.5 uur). Omdat er dan ook ruimschoots voedsel (insecten) aanwezig is hebben kleine strandlopers het in de kuikenfase een stuk gemakkelijker dan tijdens het bebroeden van de eieren.

Voor bonte strandlopers is het een ander verhaal. De energie-uitgaven verschillen ook hier niet tussen de incubatieperiode en de kuikenperiode. Het uitbroeden van de eieren doen ze samen, dus hebben ze ieder de helft van de tijd om voedsel te zoeken. Als de kuikens er eenmaal zijn staat het mannetje er alleen voor en in

plaats van de halve dag vrij te kunnen besteden moet hij nu de hele dag op de kuikens passen. Wordt het voor de kleine strandloper relatief eenvoudiger als de kuikens er eenmaal zijn, bonte strandlopervaders hebben het dan nog steeds even zwaar. Weliswaar is er dan meer voedsel en is het inmiddels warmer, maar ze hebben minder tijd voor zichzelf.

In het licht van deze verschillen wordt het begrijpelijk waarom steltlopers die alleen broeden later in het seizoen op de toendra aankomen en ook later beginnen met broeden dan soorten die de broedzorg delen. Later in het seizoen is het warmer, is er meer voedsel beschikbaar en is het dus gemakkelijker om in de spaarzame momenten dat ze de eieren alleen kunnen laten, genoeg te eten.



Chapter 7



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Growth and energetics of a small shorebird species in a cold environment: the little stint *Calidris minuta* on the Taimyr Peninsula, Siberia

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The little stint *Calidris minuta* is one of the smallest shorebird species breeding in the Arctic (weighing 4.3 g on hatching). Their chicks are small and have a high surface area-to-volume ratio. We determined prefledging growth, energy expenditure and time budgets for little stint chicks in northwestern Taimyr, Siberia. A modified power curve was introduced to model the relationship between daily energy expenditure and body mass. Total metabolisable energy, TME, over the 15-day prefledging period was 107% greater than the allometric prediction for a bird the size of a little stint. Their growth rate coefficient was 14% greater than the prediction for a bird their size. The growth of young chicks was reduced in cool weather, possibly due to a reduction in foraging time in order to be brooded and reduced food availability which impact foraging efficiency. We did not detect weather effects on energy expenditure of chicks, but lack of temperature variation during energy expenditure measurements may have prevented this. In sum, both growth rate coefficient and energy expenditure of little stint chicks were greater than predicted and this is similar to that observed in other arctic shorebird species.

Introduction

Migrant shorebirds experience the low temperatures and high wind velocities of the High Arctic during the summer months, May to August (Chernov 1985). The little stint *Calidris minuta* is one of the smallest shorebirds that migrates from as far as southern Africa to the Arctic (ca. 13 000 km) to breed, and their chicks are among the smallest self-feeding warm-blooded animals on the tundra, weighing 4.3 g upon hatching (Underhill et al. 1993; Schekkerman et al. 1998a). The highest breeding densities of little stints occur in the arctic tundra subzone between 72°N and 75°N in Siberia (Rogacheva 1992)

Little stint chicks are self-feeding precocials (Schekkerman et al. 1998a) and in addition to energy needed for growth and development they also require energy for locomotion and thermoregulation while foraging (Starck and Ricklefs 1998). As a result of their small size, little stint chicks have a large surface area compared to their body volume and thus lose heat rapidly in the cold (Schekkerman et al. 2003). Unlike adult birds, young chicks are incapable of maintaining their body temperature by producing sufficient heat through shivering (Dawson 1975; Visser and Ricklefs 1993; Krijgsveld et al. 2001). In addition, although the down which covers young chicks provides a measure of insulation, it is far less effective than adult plumage (Visser and Ricklefs 1993). Therefore young chicks require brooding by their parents to insulate them from the cold and to enable their body temperatures to increase by a transfer of heat from the parent after a feeding period (Kendeigh 1969; Krijgsveld et al. 2001). Chicks of small shorebird species grow relatively more rapidly than larger species (Beintema and Visser 1989b; Krijgsveld et al. 2001) and Kendeigh (1969) and Krijgsveld et al. (2001) showed that small species are capable of increasing their metabolism to a relatively higher level than large species to maintain body temperature. The fast growth of chicks of smaller species may be a result of their investing energy in growth and mature function of tissue to its maximum capacity (Krijgsveld et al. 2001).

Several studies of the energetics of free-living shorebird chicks have been completed in arctic and temperate zones (Schekkerman and Visser 2001; Joest 2003; Schekkerman et al. 2003) and these show that energy expenditure is greater in shorebirds growing at higher latitudes. We measured growth rate, daily energy expenditure (DEE) and time-activity budgets during the pre fledging period of little stint chicks in the field. We compared growth and energy expenditure of little stints with predicted values for a species of its size and to values of other arctic and temperate breeding shorebirds. We hypothesised that due to their small size and high surface area-to-volume ratio, little stint chicks have greater energy expenditure than predicted for their body size, and that environmental variation (e.g. weather) has a strong effect on their energy expenditure and time budgets and consequently impacts their growth.

Methods

Study area

Measurements were performed on birds in the vicinity of the Willem Barentsz Biological Station at Medusa Bay, (73°04'N 80°30'E), near Dikson on the northwestern Taimyr Peninsula, Siberia, Russia. All growth and energetics data were collected in June to August 2002 and time-budget data were collected in the summers of 2000 to 2002. The landscape of the 4 km² main study area is classified as arctic tundra (Chernov 1985), with the highest of the rolling hills reaching 39 m above sea level. The vegetation of the study area is mostly well-vegetated tundra (mosses, lichens, grasses, herbs and dwarf willows *Salix polaris*) with an area of large polygonal bogs to the east. Schekkerman et al. (2004) provide a more detailed description of the study area.

Weather data

Weather conditions for the study site, including ambient air temperature (T_a , °C) ca. 1 m above the ground and wind speed ($m \cdot s^{-1}$) ca. 10 m above the ground, were measured and logged every 30 minutes. Ambient air temperature at 1 m is strongly correlated with that at chicks' body levels (2-10 cm, Tulp unpubl. data). Rainfall (mm) was recorded daily.

Growth measurements

Nests were located during laying or incubation. Hatch date was estimated using floatation tests (Schekkerman et al. 2004; Liebezeit et al. 2007), and nests were monitored intensively close to the predicted hatch date. Chicks were located through observation of adults caring for chicks. The family was observed from a short distance and the positions of chicks noted, whereafter the brood was approached quickly by one observer while another person was guided to the chicks through instructions from the observer. Chicks were ringed and weighed either in the nest cup or when broods were encountered on the tundra. Throughout the prefledging period, chicks were recaptured when encountered to record their growth. Mass (to the nearest 0.1 or 0.5 g) was measured using Pesola spring balances. Chicks were released at the site of their capture.

Mean masses for hatchlings were determined in the nest and for prefledglings measured on their last capture at 14 to 15 days old. All chicks of known age with an accuracy of 24 hours and for which at least two measurements were taken, were used to describe growth of body mass. Growth parameters were determined for the Gompertz,

$$M = A \cdot \exp(-\exp(-K \cdot (t - T))),$$

and logistic,

$$M = A / (1 + \exp(-K \cdot (t - T))),$$

growth models and the fits of both growth curves were compared. In these growth models, the parameter M is body mass (g), A is the asymptotic body mass (g), K is the growth coefficient (d^{-1}), t is the age of the chick (d) at the time of the observation, and T is age at the point of inflection (d). The better fitting curve was chosen to describe the data. Chicks fledge while still increasing in mass and it is not feasible to obtain a biologically meaningful estimate of the asymptote. The asymptote of body mass, A , was fixed at the mean adult body mass observed in the study area, 26.6 g (chapter 5). The growth rate coefficient for the Gompertz curve, K_G , or the logistic curve, K_L , and the point of inflection were estimated for individual chicks through regression. The median values were taken as the growth rate coefficient and point of inflection for the species. Parameter estimations were only obtained from chicks which were presumed to fledge successfully (data from chicks that were known not to fledge were removed from the analysis), to produce a curve for "normal successful" growth.

Growth of chicks may be influenced both by temperature (affecting energy expenditure and the time available for foraging instead of being parentally brooded) and by food availability. As growth of shorebird chicks follows an S-shaped curve, we compared the growth rate coefficients of chicks at different ages and over different intervals by means of a growth index (growth observed / growth predicted over the same time interval from the fitted growth curve for little stint chicks for the 2002 breeding season (cf. Schekkerman et

al. 2003). Growth indices were determined for chicks which were captured at two to five day intervals. The growth indices were normally distributed (Kolmogorov-Smirnov test: $KS = 0.05209$, $P > 0.10$). These growth indices were used to analyse the dependence of growth rate on mid-interval date (the date midway between the first and last measurement of the chick) and ambient temperature (T_a , °C) during the recapture interval through linear regression. Since shorebird chicks often lose mass during the first day(s) after hatching and this is not reflected in the fitted standard growth curves (Schekkerman et al. 1998a; Schekkerman et al. 1998b), growth indices for chicks first weighed when less than a day old (often still in the nest) tend to be lower than those for older chicks. Therefore, we analysed the growth of neonates up to 5 g and chicks greater than 5 g at the start of the recapture interval separately.

Energetic expenditure measurements using DLW

Daily energy expenditure (DEE, $\text{kJ}\cdot\text{d}^{-1}$), defined as energy expenditure excluding that which is deposited into tissue, was measured using the doubly labelled water (DLW) technique (Lifson and McClintock 1966; Nagy 1980; Speakman 1997; Visser and Schekkerman 1999) on free-living chicks. Either single chicks or siblings in families with up to four chicks were captured, weighed to the nearest gram and then injected subcutaneously in the ventral region with 0.05 to 0.1 ml of DLW, depending on the mass of the chick. The DLW consisted of 36.7% D_2O and 59.9% H_2^{18}O . Both two-sample (Nagy 1983) and single-sample (Webster and Weathers 1989) DLW protocols were used. The little stint chicks subjected to the two-sample protocol were kept warm in a well-ventilated cloth bag containing a hot water bottle after their injection for an equilibration period of approximately one hour after which four to six 10–15 μl initial blood samples were collected from the brachial vein, into glass capillary tubes, which were flame-sealed with a propane torch within minutes. These chicks were then released to their parent which stayed nearby during processing. Chicks subjected to the single-sample protocol and were released directly after the DLW injection, and no initial blood samples were taken. Broods were relocated and chicks recaptured after approximately 24 hours, and mass measurements and final blood samples were taken. Blood samples were collected from four chicks before injection with DLW to measure background isotope levels.

$^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ ratios in the blood samples were analysed with a SIRA 9 isotope ratio mass spectrometer at the Centre for Isotope Research, University of Groningen, following procedures described by Visser and Schekkerman (1999) and Visser et al. (2000a). Due to difficulties injecting known quantities of DLW (especially in small chicks), the chick's body water pool (N , moles) was estimated using the equation for shorebird chicks (modified from Schekkerman and Visser 2001) by inserting the appropriate body mass into the function:

$$N = 0.000556 \cdot M \cdot (79.86 - (9.55 \cdot (M/26.6))),$$

where M represents the chick's body mass (g) during the DLW measurement, taken as the average of the initial and final masses, and 26.6 is the asymptotic body mass (g). Daily rates of carbon dioxide production were determined using the methods described and validated for growing chicks by Visser and Schekkerman (1999), Visser et al. (2000b) and Schekkerman and Visser (2001). Rates of carbon dioxide production were converted to DEE using a factor of 27.3 $\text{kJ}\cdot\text{l}^{-1}$ of carbon dioxide produced, based on a diet rich in protein (Gessaman and Nagy 1988). Analyses were done in triplicate and averaged.

Statistical analysis and a new model to establish the relationship between DEE and body mass

The relationship between daily energy expenditure (DEE, kJ.d⁻¹) and body mass, M (g), in growing chicks is usually modelled using the standard power curve,

$$\text{DEE} = a \cdot M^b,$$

where a represents a coefficient and b represents the allometric scaling exponent (e.g., Weathers and Siegel 1995, Schekkerman and Visser 2001, Visser and Schekkerman 1999). The standard power curve can be rewritten as a straight line in log-log space,

$$\log(\text{DEE}) = A + b \cdot \log M,$$

where A equals log a, with A (and therefore a) and b estimated by linear regression. This model assumes a single allometric scaling exponent throughout the development period. However, this model was not appropriate for the little stint data (see Results). In the past, a non-linear relationship in log-log space has been solved by applying two different power curve functions to specific phases of the postnatal period, the biphasic approach, e.g. Freeman (1967) described the resting metabolic rate of Japanese quail, *Coturnix coturnix japonica*, using the biphasic approach and Dietz and Ricklefs (1997) used this type of analysis to determine the moment in development when metabolism changed dramatically. We modified the standard power curve by adding a third parameter so that the scaling exponent becomes (b-(c/M)) and varies with body mass,

$$\text{DEE} = a \cdot M^{(b-(c/M))},$$

where a, b and c are coefficients to be estimated. This model is more parsimonious than the biphasic approach, with three parameters in place of five, and it overcomes the mathematical artefact of the break-point between the two curves. The three parameters can be estimated by standard multiple linear regression software, because it can be written in the form:

$$\log(\text{DEE}) = A + b \cdot \log M + c \cdot M^{-1} \cdot \log M$$

where A is log a and M is body mass (g). The parameters of this model cannot be directly compared to those of the standard power curve. To keep the results in this paper comparable to those of previous studies, analyses were completed using both the modified power curve and the standard power curve. The programme GraphPad Prism (Motulsky and Christopoulos 2004) was used for both regressions. Because the standard power curve and the modified power curve are nested models, we used the F-test to determine which better fits the DEE data for little stints (Motulsky and Christopoulos 2004).

The DEE data were tested for outliers using Grubb's test (Motulsky and Christopoulos 2004), and the pattern of the residuals of the regressions were tested using the Wald-Wolfowitz Runs Test (Motulsky and Christopoulos 2004). We note that the DEE data contain repeated measures for chicks and that there may be brood effects in both the DEE and the growth data. There were no clustered deviations from the fitted curve, so we used the above method to give initial insights into the data. The investigation of the effects of repeated measures and brood effects may require a larger data set and thus warrants investigation.

The impact of weather on DEE was determined through forward selection linear regression using the equation:

$$\log(\text{DEE}) = A + b \cdot \log M + c \cdot M^{-1} \cdot \log M + d \cdot T_a + e \cdot \text{wind speed} + f \cdot \text{rainfall}.$$

The additional explanatory variables were tested both untransformed, as done by Schekkerman and Visser (2001) and Schekkerman et al. (2003), and after logarithmic transformation.

Energy budget estimation

Prefledging energy budgets were constructed on the basis of the average body mass growth curve for free-living chicks. Metabolisable energy (ME) is the sum of two components: DEE and energy that is converted into tissue (E_{tis} , kJ.d^{-1}). DEE measured through the DLW method constitutes resting metabolic rate (RMR, kJ.d^{-1}), energy used for assimilation of nutrients and tissue synthesis (E_{syn} , kJ.d^{-1}), and the energy costs of thermoregulation and activity ($E_{\text{tr} + \text{act}}$, kJ.d^{-1}). RMR and $E_{\text{tr} + \text{act}}$ were not determined separately for little stint chicks, but a combined value was estimated. E_{tis} was estimated as the daily increment of the product of body mass and energy density using the equation

$$E_{\text{tis}}(t) = M_t (4.38 + 3.21 (M_t/26.6)) - M_{t-1} (4.38 + 3.21 (M_{t-1}/26.6))$$

where M_{t-1} and M_t are the masses (g) estimated by the logistic growth curve for days $t-1$ and t , and 26.6 is the asymptotic mass (g) for the species (Schekkerman and Visser 2001).

The relationship between ME and body mass was modelled using the standard power curve and the modified power curve. The impact of weather on ME was determined through forward selection linear regression using the modified power curve, as for the DEE.

Peak daily metabolisable energy (peak DME, kJ.d^{-1}) is the maximal daily energy demand of chicks across the prefledging period (Weathers 1992). Precocial birds often fledge before attaining adult mass (Fjelds  1977; Starck and Ricklefs 1998), thus their energy requirements may continue to increase after fledging. Little stint chicks fledge at 73-92% of adult mass. Total metabolisable energy (TME, kJ) was estimated as the total amount of energy metabolized during the prefledging period. Assuming a synthesis efficiency (E_{syn}) of 75% (Ricklefs 1974), total energy for growth (kJ) was estimated as the combination of daily E_{tis} and E_{syn} values across the prefledging period (i.e. $1.33 \cdot [\text{sum of daily } E_{\text{tis}} \text{ values}]$). The energy used for RMR and $E_{\text{tr} + \text{act}}$ was estimated by subtracting the total energy for growth from TME. Growth efficiency (%) was estimated as the sum of the daily E_{tis} values divided by TME.

To study the impact of the type of curve used on the estimates for peak DME and TME, energy budgets were calculated based on both the standard power curve and the modified power curve.

Time budget

Observations were made on six different broods in 2000, 2001 and 2002. Observation periods ($N = 40$) were scattered throughout the 24 hours of daylight and at all stages of chick development, from hatching to 17 days, and totalled 60.9 hours in bouts of 38-130 minutes (average 91, SD = 25 minutes). Chick behaviour was categorised as brooding, foraging, or other behaviours (including preening, walking and hiding at the adult's alarm). The proportion of total observation time spent brooding was modelled in relation to age, temperature and

whether it was 'day' (04:00 to 22:00 h local time (i.e., GMT + 3 h), the period in which light levels were generally largest in our study area) or 'night' (22:00 to 04:00 h) using multiple regression on the logit-transformed values.

Results

Environmental conditions

During the period that unfledged chicks were present, average ambient temperature, T_a , was 8.6°C (SD = 3.6, range = 4.3 - 15.4). Rainfall during the period when unfledged chicks were present was greater than recorded in the previous two summers at the same study site. As a possible result of cool temperatures and rainfall, the peak in arthropod abundance was narrow, about a week around 20 July (Schekkerman et al. 2004).

Chick growth

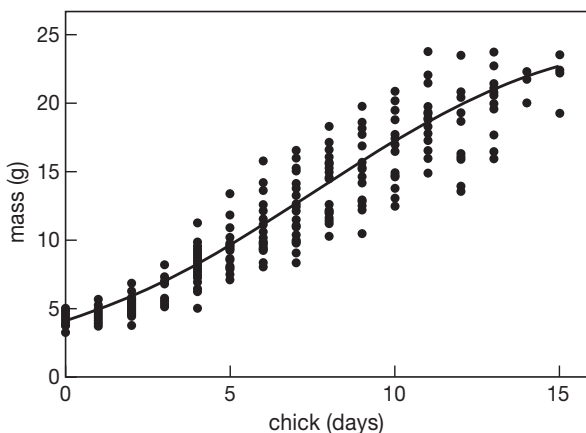
Throughout the prefledging period, 338 captures and recaptures were made of 98 chicks from 34 broods. Fifty-nine chicks were caught at least once after they were five days old. Median hatching mass of chicks found in the nest cup was 4.3 g (mean = 4.2, range = 3.2 - 4.9, SD = 0.3, N = 57). Chicks fledged when 14-16 days old (based on last capture), weighing between 19.3 and 24.4 g (mean = 22.3, SD = 1.9, N = 5). This was 73% to 92% of body mass of adult little stints, 26.6 g (chapter 5).

Although no formal test was possible, the logistic growth model seemed to fit the body mass data of little stints as well as or slightly better than the Gompertz growth model. Body mass (M, g) in relation to age (t, d) was described as:

$$M = 26.6 / (1 + \exp(-0.234(t - 7.40)))$$

($SE_{KL} = 0.006$, $SE_T = 0.169$, $n = 99$, figure 7.1).

Figure 7.1. The growth of little stint chicks at Medusa Bay in 2002. The data points show individual measurements of chicks, and the curve is the logistic growth function, $M = 26.6 / (1 + \exp(-0.234(t - 7.40)))$, based on the medians of individual fitted curve parameters; see text for method.

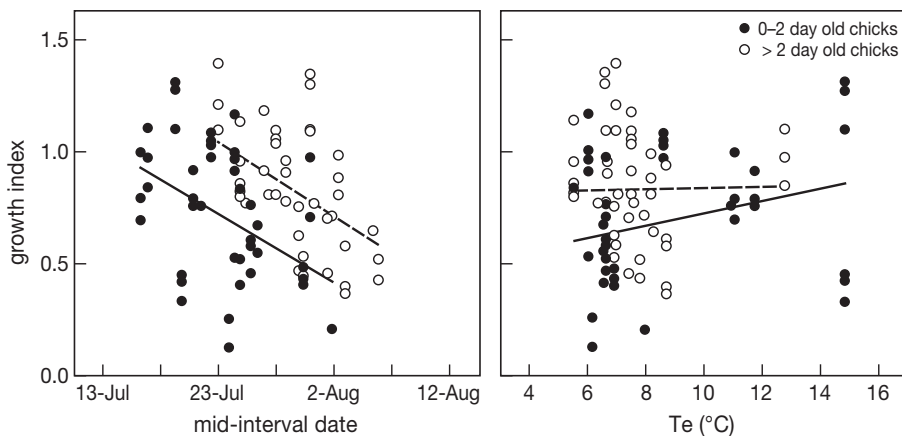


Significant negative relationships were found between the growth index and mid-interval date (table 7.1), indicating that there was a seasonal effect on growth. Chicks that hatched early in the breeding season grew faster than those that hatched later. Mid-interval date was negatively correlated to ambient temperature (Pearson Product Moment Correlation: $r = -0.565$, $N = 89$, $P < 0.001$). The growth index was positively related to ambient temperature (T_a , °C) in young chicks up to two days of age, but not in older chicks (figure 7.2, table 7.1¹). The results using the different growth indices indicate that little stint chicks in Medusa Bay in 2002 did not grow as rapidly as has been observed in this species previously.

Table 7.1. Growth index of body mass in free-living little stint chicks at Medusa Bay in 2002 and mid-interval date (middle date between first and last measurement), and ambient temperature, T_a : for more detail see text and Figure 7.2.

age of chicks	predictor variable	regression coefficients \pm SE		R^2	P
		constant	predictor		
all	mid-interval date	1.392 ± 0.195	-0.017 ± 0.007	0.061	0.020
0–2 days	mid-interval date	1.486 ± 0.263	-0.041 ± 0.011	0.232	0.001
>2 days	mid-interval date	1.918 ± 0.408	-0.032 ± 0.014	0.116	0.027
all	T_a	0.731 ± 0.124	0.024 ± 0.014	0.031	0.091
0–2 days	T_a	0.503 ± 0.154	0.041 ± 0.015	0.135	0.011
>2 days	T_a	1.293 ± 0.436	-0.043 ± 0.059	0.012	0.472

Figure 7.2. Growth index over recapture intervals of little stint chicks at Medusa Bay in 2002, in relation to (A) mid-interval date and (B) mean ambient temperature.



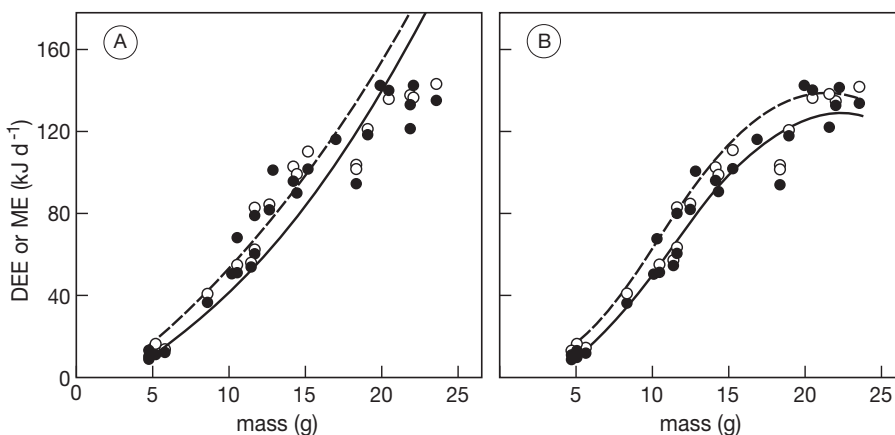
1 A more conservative reanalysis carried out later, in which individual measurements on the same chick were not treated as independent datapoints did not result in a significant effect (see chapter 8).

Energy expenditure

Twenty-nine measurements of DEE were made on 22 free-living chicks from eight broods. Seven chicks had two measurements made on them, at intervals of at least four days. In the 21 cases when the two-sample protocol was used, the initial blood sample was taken after an equilibration period of 0.50 to 1.27 hours (mean = 0.81, SD = 0.18). Final blood samples of these chicks were taken 24.0-24.1 hours after the initial samples were taken (mean = 24.0, SD = 0.02, N = 21). Eight DLW measurements were taken using the single sample method; three of these were for three repeated measurement chicks and five were completed on small chicks weighing less than 6 g. These chicks were sampled 24.0-24.1 hours after injection (mean 24.0, SD = 0.02, N = 8). During all experiments, chicks gained mass at an average rate of 0.82 g.d⁻¹ (range = 0.10 - 3.50, SD = 0.74, N = 29). The mean growth index over the DLW measurement interval was 0.97 (SD = 0.040, range = 0.39 - 1.39, N = 29), hence the DLW chicks grew as fast as other chicks in the field.

The DEE data showed a normal distribution with no outliers. The standard power curve relationship between DEE (kJ.d⁻¹) and body mass (M, g) was: $DEE = 0.655 \cdot M^{1.793}$ (figure 7.3a) ($R^2 = 0.937$, $SE_a = 1.256$, $SE_b = 1.227$, N = 29). This power curve tended to underestimate DEE in chicks of 10 to 15 g, and to overestimate DEE in chicks heavier than 20 g (figure 7.3a). The Runs test showed that the data did not follow the standard power curve (Runs test: $N_1 = 16$, $N_2 = 13$, U = 6, P < 0.001). The inclusion of an additional term to form the modified power curve significantly improved the fit (F-test: F = 62.0, df = 1, 26, P < 0.0001): $DEE = 10^{13.30} \cdot M^{-5.610} \cdot (60.02/M)$ (figure 7.3b) ($R^2 = 0.981$, $SE_a = 51.76$, $SE_b = 7.625$, $SE_c = 0.942$, N = 29). The residuals of the modified power curve were evenly distributed along the fitted curve through the body mass range (Runs test: $N_1 = 15$, $N_2 = 14$, U = 12, P > 0.1).

Figure 7. 3. The relationship between daily energy expenditure (DEE, kJ.d⁻¹) and daily metabolisable energy (ME, kJ.d⁻¹), with body mass (g) of little stint chicks at Medusa Bay in 2002 described by (A) the standard power curve and (B) the modified power curve. The solid circles and solid line represent the DEE data and the fitted allometric relationship, and the open circles and dotted line represent the ME data and the fitted allometric relationship.



According to the modified power curve daily energy requirements of little stints increased during the prefledging period, from 8.0 kJ.d⁻¹ in the first day after hatching to 128.0 kJ.d⁻¹ in a 22.4 g chick that was close to fledging (i.e. aged 15 days).

The average ambient temperature at Medusa Bay during the DEE measurements was 7.8°C (range = 5.1–10.3, SD = 1.22, N = 29), mean wind speed was 7.1 m.s⁻¹ (range = 4.9–8.9, SD = 1.36, N = 29) and mean rainfall was 2.7 mm (range = 0.0–7.0, SD = 2.66, N = 29). The fit of the modified power curve was not significantly improved through the inclusion of T_a (P = 0.315), wind speed (P = 0.221) or rainfall (P = 0.318) during the DLW measurement. Log-transforming the weather variables before inclusion in the regression did not change the results.

Energy budget

The relationship between ME (kJ.d⁻¹) and body mass (M, g) can be described by the standard power curve, $ME = 1.0859 \cdot M^{1.651}$ (figure 7.3a) ($R^2 = 0.943$, $SE_a = 1.219$, $SE_b = 0.078$, N = 29). The inclusion of the additional term to form the modified power curve resulted in $ME = 2.333^{11} \cdot M^{-4.585 \cdot (50.564/M)}$ (figure 7.3b) ($R^2 = 0.945$, $SE_a = 39.719$, $SE_b = 0.878$, $SE_c = 7.113$, N = 29). According to the F-test, the standard power curve was the better fitting model (F-test: F = 2.91, df = 1, 26, P < 0.0999). The residuals of the standard power curve were, however, distributed in clumps along the fitted curve (Runs test: N₁ = 11, N₂ = 18, U = 8, P < 0.01). The residuals of the modified power curve were more evenly distributed through the body mass range (Runs test: N₁ = 13, N₂ = 16, U = 12, P > 0.05). Thus we chose to use the modified power curve for these data also.

The fit of the modified power curve was not significantly improved by the inclusion of T_a (P = 0.166), wind speed (P = 0.576), or rainfall (P = 0.274) over the ME measurement period or the logarithm of these variables.

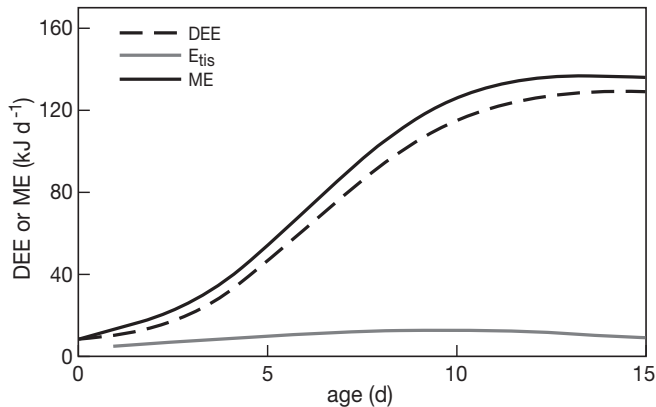
Peak DME (at 15 days) of little stint chicks was 137.1 kJ.d⁻¹ (figure 7.4, table 7.2), and TME over the 15-day prefledging period was 1348.4 kJ (table 7.2). Growth efficiency of little stint chicks up to 15 days old was 11%; 14% of TME was allocated to growth and 86% to RMR and E_{th+act}. Peak DME and TME estimated using the standard power curve were greater than

Table 7.2. Energy budget results from the standard power curve and the modified power curve describing the relationship between body mass and DEE for little stint chicks at Medusa Bay in 2002.

	standard power curve	modified power curve
peak DME (kJ.d ⁻¹)	185.9	137.1
TME (kJ)	1413.8	1348.4
relative Peak DME (% above the prediction)	196.6	118.8
relative TME (% above the prediction)	116.9	106.9
total energy accumulated (kJ)	142.7	142.7
energy of heat produced in biosynthesis (kJ)	47.5	47.5
total energy for growth including biosynthesis (kJ)	190.2	190.2
growth efficiency (%)	10.1	10.6
total energy for growth (%)	13.5	14.1
total energy for RMR, Eth+act (%)	86.5	85.9

those estimated by the modified power curve (table 7.2). This is a result of overestimations by the standard power curve in larger chicks (figure 7.3a). Average daily metabolisable energy, (ADME), which is TME divided by both fledging mass (g) and time to fledging (d, Weathers 1992), was $3.95 \text{ kJ.g}^{-1}.\text{d}^{-1}$ for little stint chicks.

Figure 7.4. Prefledging energy budgets for free-living little stint chicks at Medusa Bay in 2002 growing at an average rate from hatching to fledging. Components shown are daily energy expenditure (DEE), energy in tissue (E_{tis}) and metabolisable energy intake (MEI).



Time budget

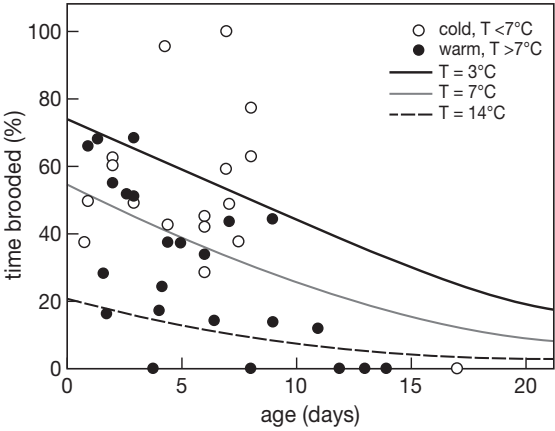
Chicks up to one week old spent an average of 46% (SD = 23, N = 28) of their time brooding and 52% of their time foraging (SD = 22, N = 28). Chicks older than one week spent 21% (SD = 27, N = 12) of their time brooding and 76% of their time foraging (SD = 27, N = 12). Other activities, including preening, walking and vigilance, were observed for only 2% (SD = 4) of the time during the first week and 3.5% thereafter. Little stint chicks therefore spent most of their “unbrooded” time foraging.

The proportion of time brooded decreased significantly with increasing age and with increasing temperature (table 7.3, figure 7.5). The regression lines in figure 7.5 overestimate the brooding times of older chicks as few observations were made on chicks older than 12 days which effectively no longer require brooding. In addition there was a tendency for brooding time to be increased between 22:00 and 04:00 hours, indicative of a circadian activity rhythm with sleep accommodated into night-time brooding bouts, but this was not significant ($P = 0.17$), probably as a consequence of the small sample size for “night” relative to “day”. Interactions between age, temperature and ‘night’ proved not significant (all $P > 0.41$), nor were additional effects of wind ($P = 0.35$), or rainfall ($P = 0.15$), if included in a model containing age and temperature. Results were very similar if body mass was used as a predictor of brooding time instead of age (table 7.3).

Table 7.3. Regression analysis for brooding time of little stint chicks at Medusa Bay in 2000, 2001 and 2002. Modelled with (A) age and (B) body mass. F-probabilities are for terms sequentially added to the model; estimates (logit proportion of time brooded) are for the final model including all variables.

variable added	df	change in deviance	deviance ratio	F-probability	estimate (logit)	SE
A						
constant		2.7718			1.674	0.501
age	1	0.6881	19.87	<0.001	-0.1250	0.0476
temperature	1	0.7082	20.45	<0.001	-0.2182	0.0623
'night'	1	0.0676	1.95	0.171	0.473	0.345
residual	36	1.3756				
B						
constant		2.7718			1.839	0.544
mass	1	0.4807	12.41	0.001	-0.0878	0.0349
temperature	1	0.8155	21.06	<0.001	-0.2217	0.0626
'night'	1	0.0993	2.56	0.12	0.574	0.356
residual	36	1.3763				

Figure 7.5. Percentage of time little stint chicks at Medusa Bay in 2002 spent being brooded in relation to age (d) and air temperature (°C), (regression lines shown for the lowest, mean and highest air temperatures during observations).



Discussion

A new function to describe energy expenditure

The modified power curve with a gradually changing allometric scaling exponent provided a significantly better fit to the daily energy expenditure (DEE) versus body mass relationship than the standard power curve with a constant scaling exponent. In shorebird neonates, mass-specific resting metabolic rate (RMR) is at about 50% of the level observed in adult non-passerine birds (Visser and Ricklefs 1993). During early postnatal growth RMR increases rapidly with increasing body mass (intraspecific allometric scaling exponents being about 2 initially and about two thirds thereafter) to approach adult levels. In the past, multiphasic analyses have been performed in an attempt to describe these changes in RMR (Dietz and Ricklefs 1997), but it is unlikely that changes in the RMR versus body mass relationship occur instantly at a specific body mass. In free-living chicks, DEE versus body mass relationships may exhibit an even more pronounced pattern than RMR versus body mass, because the aforementioned changes in RMR are accompanied by major behavioural changes, e.g. in the time spent actively foraging. Because both physiological and behavioural changes occur gradually, the changes in DEE with increasing body mass are better described by a model containing gradual change in the allometric scaling exponent, like the modified power curve.

According to Tulp et al. (chapter 6.) adult little stints in Medusa Bay have a DEE of 154–160 kJ.d⁻¹ during incubation and chick rearing. The modified power curve for chicks predicts a DEE of 124 kJ.d⁻¹ at adult body mass (26.6 g), ca. 20% below measured adult values. Given the differences in behaviour between adults and chicks (e.g. energy-demanding flights are not made by chicks) this seems a reasonably close match. Extrapolation of the standard power curve results in a value that exceeds the prediction for adults by 145%. The better fit of the modified power curve will therefore also improve the estimates for peak daily metabolisable energy (peak DME) and total metabolisable energy (TME) of little stint chicks (table 7.2).

The biphasic approach estimates a break-point between the two models that is a mathematical artefact rather than a distinct physiological event. Weathers and Siegel (1995) analysed chick RMR of 25 species (from 31 studies) including 6 passerine and 19 non-passerine species. They found that biphasic analysis did not adequately describe the metabolism of four out of 15 non-passerine precocial and semi-precocial species included in their analysis. In addition, this method would require five estimated parameters; four for the two power curves and one for the break-point between them. The modified power curve contains only three.

Little stint chick energetics

Our estimates of prefledgling metabolism in little stint chicks, as summarised in values for peak DME and TME can be compared to those of other birds by contrasting them to allometric predictions based on fledgling body mass (M_f , g) and the length of the prefledgling period (t_f , days, Weathers 1992):

$$\text{predicted peak DME} = 11.69 \cdot M_f^{0.9082} \cdot t_f^{-0.428},$$

and

$$\text{predicted TME} = 6.65 \cdot M_f^{0.852} \cdot t_f^{0.71}.$$

Observed peak DME and TME of little stint chicks were 119% and 107% greater than predicted, respectively. Schekkerman et al. (2003) found that the observed TME of red knots at 75°N was 89% above the predicted value and that this large relative TME conformed to that observed in other arctic breeding bird species. As observed in little stint chicks of this study, the ADME of arctic breeding red knots was also large, 2.58 kJ.g⁻¹.d⁻¹ (Schekkerman et al. 2003). Therefore little stint chick energetics showed similar traits to that observed in other arctic breeding birds with precocial young.

Shorebird chicks in the Arctic grow rapidly in comparison to the expected growth rates for their size (Schekkerman et al. 1998a; Schekkerman et al. 1998b; Schekkerman et al. 2003), and precocial chicks in cooler temperatures exhibit greater overall energy expenditure than expected as a result of increased metabolism (Visser and Ricklefs 1993). Krijgsveld et al. (unpubl. data) found that the chicks of smaller arctic shorebirds had a greater mass-specific DEE than larger species, indicating a higher metabolic capacity (DEE versus RMR) than chicks of larger species.

The fast growth and large energy expenditures of shorebird chicks at high latitudes can only be sustained through sufficient food intake. Lack (1968) suggested that the abundance of arthropods increased with latitude. Schekkerman et al. (2003) found no significant difference in arthropod availability between the arctic tundra at Cape Sterlegov, and a temperate meadow in The Netherlands. The higher intake rate of red knot chicks was tentatively attributed to the simpler structure of the tundra vegetation and a larger proportion of wingless or slow-moving arthropods making prey capture easier. This may also apply to little stint chicks.

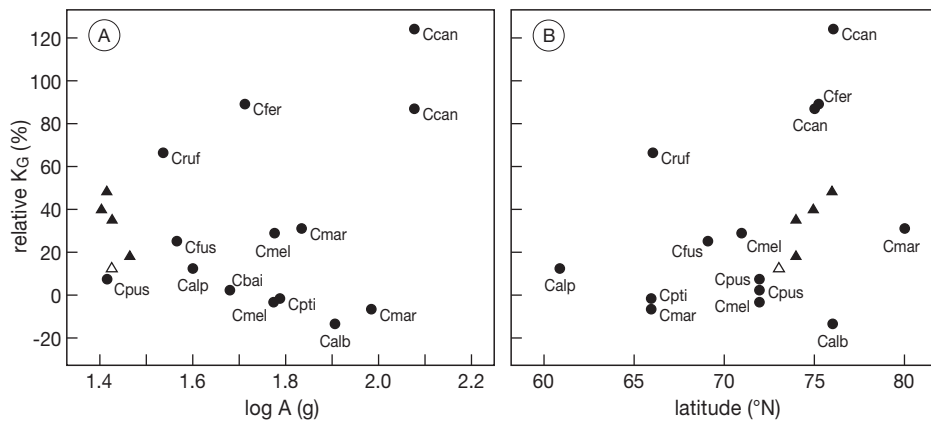
The impact of environmental conditions on energy expenditure, time budgets and growth of little stint chicks

The growth rate of shorebird chicks can be influenced by bouts of cold and wet weather (Beintema and Visser 1989a). Schekkerman et al. (1998b, 2003) found that cold weather resulted in a reduction of growth rate in curlew sandpipers and red knots. The growth of little stint chicks less than two days old was influenced by ambient temperature whereas that of larger chicks was not. Adverse weather may affect chick energy budgets in several ways: it may increase energy expenditure, reduce feeding time through an increase of brooding, and reduce feeding success through diminished insect prey availability. Although larger chicks do not suffer the same time and thermoregulatory constraints as young chicks, reduced food availability can have a similar effect on their foraging efficiency and thus their growth.

We found no significant effect of ambient temperature, wind or rain on DEE or ME. The range of mean ambient temperatures during DEE measurements was small (5-10°C) compared to the range occurring at Medusa Bay over the chick-rearing period (1-17°C, unpubl. data 2000-2002). Consequently, our sample had limited power to show such effects.

Young chicks are unable to maintain body temperature under conditions of low temperature (Norton 1973; Visser and Ricklefs 1993; Krijgsveld et al. 2003). Consequently, their mobility, rate of food intake (Krijgsveld et al. 2003) and possibly digestive efficiency (Kleiber and Dougherty 1934; Hume 2005) decrease. Young chicks seek brooding to both increase their body temperature and to reduce energy expenditure (Klaassen et al. 1992; Krijgsveld et al. 2003). Although larger chicks do not suffer the same time and thermoregulatory constraints as young chicks, reduced food availability can have a similar effect on their foraging efficiency and thus their growth.

Figure 7.6. The relationship between relative Gompertz growth rate coefficient (K_G , d^{-1}) and (A) asymptotic body mass (A , g) and (B) latitude ($^{\circ}N$) for arctic breeding sandpipers. The little stint data from Schekkerman et al. (1998a) are represented by \blacktriangle , and data from this study by \triangle . The 14 species represented in this figure by \bullet are Calb. sanderling, *Calidris alba* (Parmelee 1970 in Beintema and Visser 1989b, Glutz von Blotzheim et al. 1975), Calp. dunlin, *Calidris alpina* (Soikkeli 1975 in Beintema and Visser 1989b), Cbai. Baird's sandpiper, *Calidris bairdii* (Norton 1973 in Beintema and Visser 1989b), Ccan. red knot, *Calidris canutus* (Schekkerman et al. 2003; Tomkovich unpubl. data), Cfer. curlew sandpiper, *Calidris ferruginea* (Schekkerman et al. 1998b), Cfus. white-rumped sandpiper, *Calidris fuscicollis* (Parmelee et al. 1968 in Beintema and Visser 1989b), Cmar. purple sandpiper, *Calidris maritima* (Tomkovich 1985, Glutz von Blotzheim et al. 1975, Summers and Nicoll 2004), Cmel. pectoral sandpiper, *Calidris melanotos* (Norton 1973 in Beintema and Visser 1989b, Andreev 1988), Cptil. rock sandpiper, *Calidris ptilocnemis* (Gill et al. 2002), Cpus. semipalmated sandpiper, *Calidris pusilla* (Safriel 1975 in Beintema and Visser 1989b) and Cruf. red-necked stint, *Calidris ruficollis* (Schekkerman et al. 1998b).



In the 2002 breeding season, little stint chicks hatched late in relation to the seasonal peak in arthropod availability (Schekkerman et al. 2004), and this affected chick growth. Little stint chicks that hatched early in the breeding season grew faster than those that hatched later.

Being brooded can reduce the heat loss of chicks to the environment and thus can reduce energy expenditure. The amount of time little stint chicks spent brooding decreased with age, and chicks were rarely observed to be brooded during the day after the age of 10 days. However, neither little stint chicks (this study) nor red knot chicks (Schekkerman et al. 2003) took full advantage of the 24-hour arctic daylight period to feed.

How does the growth of little stint chicks compare to other species?

Growth rate coefficients of the different bird species described in (Rahn et al. 1984), Beintema and Visser (1989b) and others (Ricklefs 1973; Visser and Ricklefs 1993, Krijgsveld et al. unpubl. data) decrease with increased body size. Shorebird breeding seasons in the Arctic are limited by the short summers and it has been found that birds breeding in the Arctic, for instance red knots (Schekkerman et al. 2003) and purple sandpipers, *C. maritima* (Summers and Nicoll 2004), have large growth rate coefficients. The combined effect of breeding latitude and their small size may have resulted in little stint chicks exhibiting large growth rate coefficients.

The predicted Gompertz growth rate coefficient (K_G) for shorebird species with an asymptotic mass of 26.6 g using the equation $K_G = 0.390 \cdot A^{-0.312}$ (Beintema and Visser 1989b) was 0.140 d^{-1} . Assuming that the asymptotes are identical in the logistic and Gompertz models, K_L can be converted to K_G using the equation $K_G = 0.68 \cdot K_L$ (Ricklefs 1983). Following this, the little stint chicks we studied at Medusa Bay in 2002 had a K_G of 0.159 d^{-1} which is 14% above the predicted growth for a 26.6 g shorebird. The observed growth rate coefficients for individual chicks at Medusa Bay in 2002 was greater than the prediction (one sample t-test: $t = 4.12$, $df = 9$, $P < 0.001$).

Schekkerman et al. (1998a) found that little stints breeding between 72°N and 76°N in Siberia grew rapidly; with a K_G of 0.191 d^{-1} for all three sites combined (figure 7.6a). According to this pooled result little stint chicks grew 37% faster than predicted for a shorebird of 26.7 g (Schekkerman et al. 1998a). The little stint chicks we studied at Medusa Bay (73°N , 2002) also grew faster than predicted but not as fast as was observed by Schekkerman et al. (1998a). This may be a combined effect of the lower latitude of our study site, and the different environmental conditions experienced by the chicks during our study breeding seasons.

Calidrid shorebird species that breed at latitudes greater than 60°N , exhibit growth rate coefficients close to or greater than predicted by the equation of Beintema and Visser (1989b, figure 7.6b). The negative relationship between asymptotic body mass and K_G described by Beintema and Visser (1989b) may explain the large growth rate coefficients of little stints compared to that of larger shorebird species growing at similar latitudes, e.g. Baird's sandpiper, *C. biardii*, (48 g) (figure 7.6b). Some shorebird species, such as the red knot or curlew sandpiper, *C. ferruginea*, are, however, able to grow at relatively faster rates than the little stint, despite their larger asymptotic body mass.

The relative energy expenditure of little stints was greater than that of red knots (Schekkerman et al 2003), but this was not reflected in an equally large growth rate. This is most likely a consequence of their poor surface to volume ratio resulting in relatively higher thermoregulatory costs. Despite this relatively high energy expenditure they are capable of rapid growth that allows them to fledge within the short period available in the Arctic.

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Kampioenen in de kou

Jonge kleine strandlopers moeten, net als de meeste andere steltloperkuikens, vanaf de eerste dag hun eigen kostje bij elkaar scharrelen. Als ze uit het ei komen blijven ze hooguit een dagje in de nestkom liggen tot ook hun broertjes en zusjes zijn uitgekomen en opgedroogd, maar dan gaan ze definitief aan de wandel onder leiding van pa of ma, zonder nog terug te keren naar het nest. In de eerste week kunnen ze hun eigen lichaamstemperatuur nog niet op peil houden en moeten ze van tijd tot tijd worden bebroed door de ouder.

Als het erg koud is moeten kuikens vaker worden bebroed en blijft er dus minder tijd over om voedsel te zoeken. Daarbij komt nog dat bij koud weer hun energie-uitgaven hoger zijn en de beschikbaarheid van insecten afneemt. Als gevolg hiervan blijft er minder energie over voor groei, die daardoor sterk afhankelijk is van het insectenaanbod en het weer. Vergeleken met steltlopersoorten die in meer gematigde streken broeden, groeien arctische soorten echter sneller. De oorzaak hiervan is dat hun kuikens beter tegen de kou kunnen; ze kunnen langer foerageren voordat ze weer bebroed moeten worden. De tijdwinst die ze hierdoor behalen heft het temperatuurnadeel op en leidt in combinatie met het continue daglicht en – op goede dagen – een grote beschikbaarheid van vangbare insectenprooien, tot een snellere groei.

Omdat kuikens van kleine strandlopers zo klein zijn (c. 4 g bij geboorte, ter vergelijking: krombekstrandloper: 8-9 g en bonte strandloper 7-8 g) hebben ze meer en tot op latere leeftijd bebroeding nodig dan kuikens van grotere soorten. Die bebroedingstijd gaat ten koste van de foerageertijd. Door observaties hebben we vastgesteld dat kuikens in hun eerste levensdagen afhankelijk van het weer overdag ruim 60% van de tijd worden bebroed en 's nachts nog meer. Dit neemt in de loop van de eerste week sterk af en na 10-12 dagen worden ze nauwelijks nog bebroed.

Met behulp van de zwaar water methode hebben we de energie-uitgaven van kleine strandloperkuikens van verschillende leeftijden gemeten. Vergeleken met andere arctische soorten geven kleine strandloperkuikens meer energie uit terwijl ze relatief niet sneller groeien. Dat wordt waarschijnlijk veroorzaakt door de verhouding tussen oppervlakte en inhoud die voor kleine soorten ongunstig is met

name in koude gebieden. Met relatief meer oppervlakte gaat er namelijk meer warmte verloren.

Er zit dan ook een grens aan de plekken waar kleine strandlopers nog kunnen broeden. Heel noordelijk in de zogenaamde arctische woestijn (boven 75°N) komen ze niet meer voor. De soorten die nog wel noordelijker kunnen broeden zoals kanoetstrandloper en steenloper zijn een stuk groter.



Chapter 8



Ingrid Tulp

Hans Schekkerman

Correlates of growth rates in arctic shorebird chicks: daily weather and food abundance

Unpublished manuscript



Arctic shorebirds breeding in Siberia are facing highly variable breeding conditions. Hatching success is largely determined by predation pressure, which varies in a three year cycle, depending on lemming abundance. Breeding productivity is further influenced by weather and food availability for the self-feeding chicks. Breeding success in terms of number of chicks fledged is difficult to measure in arctic breeding shorebirds due to their cryptic behaviour and extreme camouflage. But growth rate is likely to be a good proxy for breeding success as it affects both the birds' condition and the length of the period in which chicks are most vulnerable. As a follow up of two studies in which relationships between growth of chicks and environmental conditions were investigated in curlew sandpiper *Calidris ferruginea* and red knot *Calidris c. canutus*, we explored these patterns in two congeneric but smaller shorebird species: dunlin *Calidris alpina* and little stint *Calidris minuta* in 2001 and 2002 in Taimyr, Western Siberia. In 2001 growth of dunlin and little stint chicks was found to depend on hatch date, temperature, wind speed and food abundance. These effects were partly aliased, but models with combined effects explained additional variation. Despite a larger sample size, effects of hatch date and weather were not significant in 2002. As a crude estimate of the survival of chicks, the probability to resight broods that were ringed 2 days or later after ringing, showed a decline in course of the season in 2001, indicating that the declining arthropod availability affected chick survival. In parallel with the effects on growth rate also here no seasonal decline in chick survival was found in 2002. The fact that seasonal and weather-related effects were found in 2001 but not in 2002 is correlated with a very late start of the season in 2002, that has lead to a highly synchronised breeding season and little variation in food abundance over the period of measurement. That two summers already show such contrasts illustrates the enormous variation in opportunities for successful reproduction in the capricious environment of the high Arctic.

Introduction

Reproductive success in birds that breed in the arctic tundras of Siberia is highly variable (Underhill et al. 1993). One of the main driving forces behind this is the lemming abundance. Being the most important prey for predators, their abundance determines whether bird nests and chicks suffer from predation or are ignored by birds of prey and arctic foxes *Alopex lagopus*, because lemmings are generally more profitable prey when abundant. Several studies have already shown the correlation between breeding success of shorebirds and geese and indices of lemming abundance (Summers 1986; Summers and Underhill 1987; Underhill et al. 1993; Blomqvist et al. 2002).

However, breeding success is not guaranteed at low predation pressure. Arctic shorebird chicks feed themselves from their first day of life onwards on arthropods living on the tundra surface. This is a food source that shows strong seasonality and weather-dependence (chapter 9). In the first days the chicks can not maintain body temperature and need to be brooded at regular intervals (Visser and Ricklefs 1993). They are guided by one or two parents and feeding periods are alternated with brooding bouts throughout the day, with a period of continuous brooding during the coldest night time hours (even though feeding could be continued due to 24 hr daylight, Schekkerman et al. 2003b). At low temperatures feeding time is further limited because chicks cool down more rapidly and brooding time increases (Beintema and Visser 1989a; Visser and Ricklefs 1993). In such conditions energy expenditure for thermoregulation and activity is greater (Krijgsveld et al. 2003; Schekkerman et al. 2003b) while intake rate is reduced through lower arthropod availability (chapter 9).

Given the caprices of arctic weather and limited time window available for breeding, weather conditions in the chick period can be an important factor influencing reproductive success. In a study where breeding output in curlew sandpiper *Calidris ferruginea* was investigated using a 18 year dataset of juvenile percentages in South-Africa, it was shown that after correction for 'high predation' years, the remaining variation could largely be explained by the weather in the chick period in the breeding area (Schekkerman et al. 1998b). Similarly, dunlin *Calidris alpina* juvenile percentages wintering in Wales showed a strong correlation with summer temperature in the breeding area in northwestern Siberia, but not with rainfall (Beale et al. 2006). Chick survival and number of chicks fledged per breeding pair are very hard to measure in the field in most arctic shorebird species due to their mobility, inconspicuous behaviour and terrific cryptic plumage of the young in a vast expanse of habitat and in some species even the premature leaving of the parent. Growth rate may be a good proxy of fledging success, as it affects the birds condition and the length of the risky period.

Growth rates in chicks have been shown to be dependent on temperature and food availability in two arctic shorebird species, curlew sandpiper and red knot *Calidris c. canutus* (Schekkerman et al. 1998b; Schekkerman et al. 2003b). While in temperate breeding shorebirds the correlation of growth with weather has been demonstrated (Beintema and Visser 1989a; Beintema and Visser 1989b; Pearce-Higgins and Yalden 2002), a possible relationship with food has been suggested (Elias et al. 2000) but never quantified. To test whether this pattern is robust across species and years and whether the dependency of growth on weather and food is stronger in smaller species, we measured chick growth in relation to weather and food availability in two other, smaller arctic shorebird species (little stint *Calidris minuta* and dunlin *Calidris alpina*) in a three year program on the Taimyr Peninsula in Western Siberia, Russia. Of all species of which daily energy expenditure is measured to date, little stints were shown to have the relatively highest Daily Energy Expenditure (DEE,

Piersma et al. 2003). Therefore we expect that chicks of this species, that is one of the smallest breeding in the Arctic, are more sensitive to variation in food and temperature. During the first of the three years, predation pressure was so high, that only very few nests survived till hatching. In the other two years enough nests survived (mean nest survival rate of 0.19 and 0.59 in 2001 and 2002 respectively, Schekkerman et al. 2004) to be able to carry out measurements on chick growth. Instead of estimating breeding success in number of fledged chicks per pair, we used a crude measure of brood survival to investigate if there is a relationship between birth date and probability of survival.

Methods

Study site

Data were collected in June-early August 2001-2002 at Medusa Bay, in the west of the Taimyr peninsula, Siberia (73°20'N 80°30'E). The habitat consists of arctic tundra (cf Chernov 1985). Vegetation consisted of moss, lichen, grass, sedges, herbs and dwarf shrubs *Salix* spp, generally not higher than 20 cm with a significant proportion of the surface bare ground. The landscape is characterised by a rolling relief with scattered stony ridges, wet valleys with marshes and drier slopes and hilltops. During the complete study period there was continuous daylight. For a more detailed description of study area we refer to Schekkerman et al. (2004).

Weather

Air temperature, wind speed, wind direction and precipitation were recorded every 30 minutes at our study site using an automated weather station. Air temperature was recorded at 1 m height in the shade, wind speed and direction at 10 m height. Precipitation was measured in mm/day.

Arthropod abundance

The abundance and activity of surface-active arthropods was monitored using pitfall traps. Two lines of ten white plastic jars (ø 11 cm, 10 cm deep) were placed along two line transects at intervals of 5-10 m, one in moderately dry polygonal tundra, the other in relatively wet sedge dominated marsh tundra. The pitfalls were filled with 1-2 cm formaldehyde solution (4%) and a drop of detergent to reduce the surface tension. The traps were emptied every evening around 2300h and sorted and measured in the camp immediately or on the next day. If jars were flooded due to rainfall or thawing, they were discarded and data were corrected for differences in number of jars. Arthropod dry mass was calculated using the length-dry mass relationships given for different orders in Rogers et al. (1977) and Schekkerman (1997). For orders for which no specific relationship could be found, a general relationship for arthropods (Rogers et al. 1976) was used.

Chick growth rate

Nests were usually located during incubation by looking for nest-indicative behaviour of the attendant birds. Expected timing of hatching was estimated based on the floatation method (Liebezeit et al. 2007). On the expected hatching date, nests were visited to ring and measure the newly hatched young. Afterwards, chicks were retrapped whenever a known family (with colour-ringed adult) was encountered and new families (of which we did not find the nest) were also caught and ringed. Chicks of known families were recaptured at intervals of several days to measure their growth (body mass, bill, wing length).

Chick growth rate was measured in little stint and dunlin. Little stint chicks were more easily (re)captured than chicks of most other shorebird species due to their parents' tameness, although trapping became more difficult in older chicks. Little stint families generally congregate in the low-lying wet areas and usually do not wander over distances of more than a few hundred meters. Dunlin families behave less boldly and chicks are often extremely hard to find. We used the alarm calls and distraction behaviour of the parent as a cue for the presence of chicks.

Because mass growth is not linear but follows an S-shaped curve, growth rates of chicks measured at different ages and over different intervals cannot be compared directly. Therefore, growth rates were transformed to an index, by dividing the observed growth by the growth expected over the same interval from a published logistic growth curve for little stint (Scheckerman et al. 1998a). The advantage of this curve is that it is compiled over many study sites and many years and provides a good baseline for comparison. For arctic breeding dunlin there is no published growth curve available. Therefore we had to use a logistic growth curve fitted to our (limited) data of chicks of known age for dunlin and an asymptote of 46.4 g (the average mass of fledged juvenile dunlin before departure). Hence, a growth index of 1 means that chicks grew as fast as expected from this curve, while 0 denotes that chicks did not grow at all, and negative values indicate mass loss. These growth indices were used to analyse the dependence of growth rate on temperature and food availability during the recapture interval. Since shorebird chicks often lose mass during the first day(s) after hatching, which is not reflected in the logistic growth curves, growth indices for chicks first weighed when less than a day old (often still in the nest) tend to be lower than those for older chicks. Therefore, we distinguished neonates (< 5 g, resp. < 8 g at start of recapture interval in little stint and dunlin respectively) from older chicks in the analysis.

The date midway every interval (mid-interval date) was used for the time axis. In the small chicks of little stints and dunlin (weighing only 4 g resp. 7 g at hatching), measurement error in short intervals can be relatively large. If chicks were recaptured on consecutive days, we merged 1 day intervals with the adjoining 1 or 2 day interval to arrive at 2 or 3 day intervals. If a chick had only been recaptured once (on the day after ringing), this adjustment was not possible and we used the 1 day interval.

Brood survival

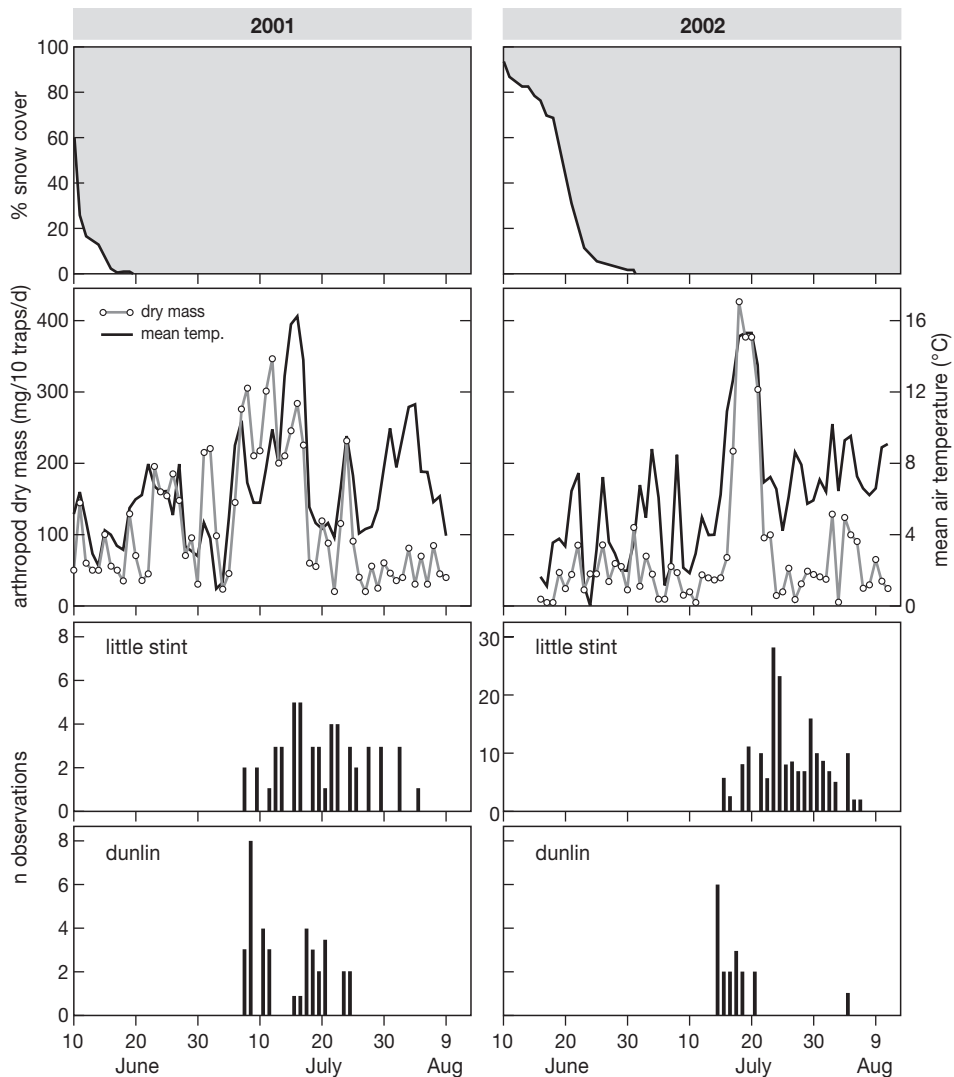
As a crude measure of brood survival, we used the probability that a brood of small chicks was recaptured or seen again (recognised by colour-marked adult) two days or more after the initial capture. If chicks could not be seen, the distraction behaviour of the parents (alarm calls) was used as a cue to determine if one or more chicks were still alive. Especially in broods with older chicks, that do not need brooding so often, chicks are not easily seen and it is very difficult to count exact numbers of chicks in each family. Up to the last days of July, the study area was searched almost every day, especially the sites that were most preferred by broods (marshes, valleys with streams). Hence, while an absence of repeat observations for a brood is no proof that the chicks did not survive for long, it certainly is an indication.

Statistical analyses

Growth rates of chicks may be influenced both by the availability of surface-active arthropods (affecting feeding success) and by weather (affecting energy expenditure and the time available for foraging instead of being brooded by a parent). For every growth interval the

mean air temperature, wind speed, mean arthropod mass and the sum of total rainfall were calculated. All these parameters are strongly correlated with date. Because these parameters cannot be separated in one analysis, we first tested whether there was an effect of date (mid-interval date) and then the effect of weather (temperature wind speed and rain) and arthropod mass in separate analyses. To investigate if arthropod mass and weather variables explained additional variation, we used a forward stepwise procedure to test the significance of these variables in combination in yet another analysis.

Figure 8.1. From top to bottom: snow cover, mean air temperature and arthropod abundance and the number of observations on chick growth for little stint and dunlin in relation to date in 2001 and 2002.



To analyse the effect of food availability, temperature and mid-interval date on chick growth rate, Linear Mixed Models were used, taking into account different levels of variation in the observations (multiple observations on several chicks from the same brood). Nest and chick were entered as random effects and arthropod dry mass, temperature, wind speed, rain or the mid-interval date as fixed effects. Apart from arthropod mass entered as a linear term, we also tried this parameter log-transformed to allow for a possible curvilinear function. However, in all analyses untransformed arthropod mass gave a better fit than log arthropod mass. Separate analyses were carried out per species and year testing for differences between age-group (0-2 days, 'young chicks' and > 2 days, 'old chicks') by including them in the fixed effects (both singly and in interaction to test for differences in intercept and slope). If an explaining variable was not significant, we repeated the analyses on the separate age groups to test if it was significant in one of the age groups.

The probability of resighting a brood that has been ringed after a period of at least two days was analysed using logistic regression. Data for both species were analysed separately for the two years. All analyses were carried out in Genstat 8.

Results

Weather and arthropod availability in the two seasons

The two seasons differed in amount of snow cover early in the season and the speed of snowmelt (figure 8.1). Upon arrival on 5 June in 2001 more than 90% of the area was still covered in snow. Because of a relatively warm June, the snow melted rapidly and reached 25% cover on 11 June and 10% on 16 June. In 2002 almost the whole area was still covered by snow upon arrival. Only at hilltops and ridges small windblown patches were free of snow. Because of low temperatures until mid June, the snow melted away much slower than in 2001. On 19/20 June snow cover was much reduced by heavy rain. Only on 23 June the snow cover reached 10% cover. Mean daily air temperature was 4.6°C in the incubation period (15 June-6 July) and 7.2°C during the chick period (3 July-10 August) in 2001. In 2002 mean temperatures were 3.9°C during incubation (23 June-14 July) and 8.5°C (14 July-18 August) during chick-rearing. The year 2002 was distinctly less sunny. Also the amount of precipitation differed markedly between the years: 59 mm rain was recorded between 6 June and 9 August in 2001, compared to 132 mm in the same period in 2002. Daily average wind speed was mostly between 2 and 10 ms⁻¹ in both years. Arthropod mass showed a strong seasonal pattern and close correlation temperature in both years (figure 8.1, see chapter 9 for detailed analyses). Variation in arthropod abundance in 2001 was much larger than in 2002, especially in the period when most chick growth measurements were taken.

Growth rate in little stint

In the analysis including both age groups there was no seasonal trend in growth index. However, when analysed separately, young chicks showed a significant seasonal decline in growth rate (table 8.1). In 2001 growth rate was positively correlated with temperature, arthropod availability and rain and negatively to wind speed when tested in separate analyses (figure 8.2, table 8.1). Different intercepts (tested by including the age groups) were found in the relations between growth index and mid-interval date, temperature and arthropod mass (table 8.1). In addition, also the slope differed between the age groups in the relation between growth index and temperature and between growth index and arthropod mass (figure 8.1, table 8.1). After entering temperature first, additional variation could be explained by wind speed and arthropod mass (table 8.1), but this model did not differ for the two age groups.

Despite the larger sample size in 2002, there was neither a significant seasonal effect nor an effect of any of the weather variables or arthropod mass on chick growth in both age groups combined or separate (table 8.1). Judging from the plot (figure 8.2) a curvilinear relationship would be expected, but a ln-transformation of the explanatory variables did not show it. There was, however, a tendency for the lower growth rate extremes to coincide with late dates, low temperatures and low arthropod mass.

Table 8.1. Results of Linear Mixed Models to analyse the effect of mid-interval date, temperature, wind speed, rain and arthropod mass on growth (growth index) of little stint chicks. Nest/brood and ring number were entered as random variables. Because of the correlation between the weather-related variables and mid-interval date, these were analysed separately. For every year the effect of mid-interval date was investigated and in separate model the effect of temperature and arthropod mass. Models were first run for both age groups combined; if no effect was found separate analyses were run for each age group.

year	N	age group	model	Wald	P	effect	SE
2001	49	all	mid-interval date	not significant			
		age 0-2 days		6.32	0.0120	-0.0635	0.0253
		age > 2 days		not significant			
		all	temperature	15.39	<0.001	0.2569	0.0379
			age	11.57	<0.001		
			temperature.age	35.06	<0.001		
			age 0-2 days			0.0000	0.0000
			age > 2 days			-0.0828	0.1004
		all	wind speed	11.64	<0.001	-0.1107	0.0325
		all	rain	6.41	0.011	0.1587	0.0627
		all	arthropod mass	5.90	0.015	0.1781	0.0266
			age	37.05	<0.001		
			arthropod mass.age	18.02	<0.001		
			age 0-2 days			0.0000	0.0000
			age > 2 days			0.4173	0.0990
2002	158	all	temperature	13.47	<0.001	0.0035	0.0229
			wind speed	18.35	<0.001	-0.1962	0.0310
			arthropod mass	22.74	<0.001	0.1302	0.0273
		all	no significant relations				
		all					

Figure 8.2. Growth index over recapture in relation to mid-interval date, arthropod availability, and mean temperature for little stint in 2001/2002. For the explanation of growth index see text. Lines are regression lines for the linear regressions and are only presented if the explaining variable is significantly related to growth rate (lines for 0-2 days old chicks, dotted lines for chicks > 2 days).

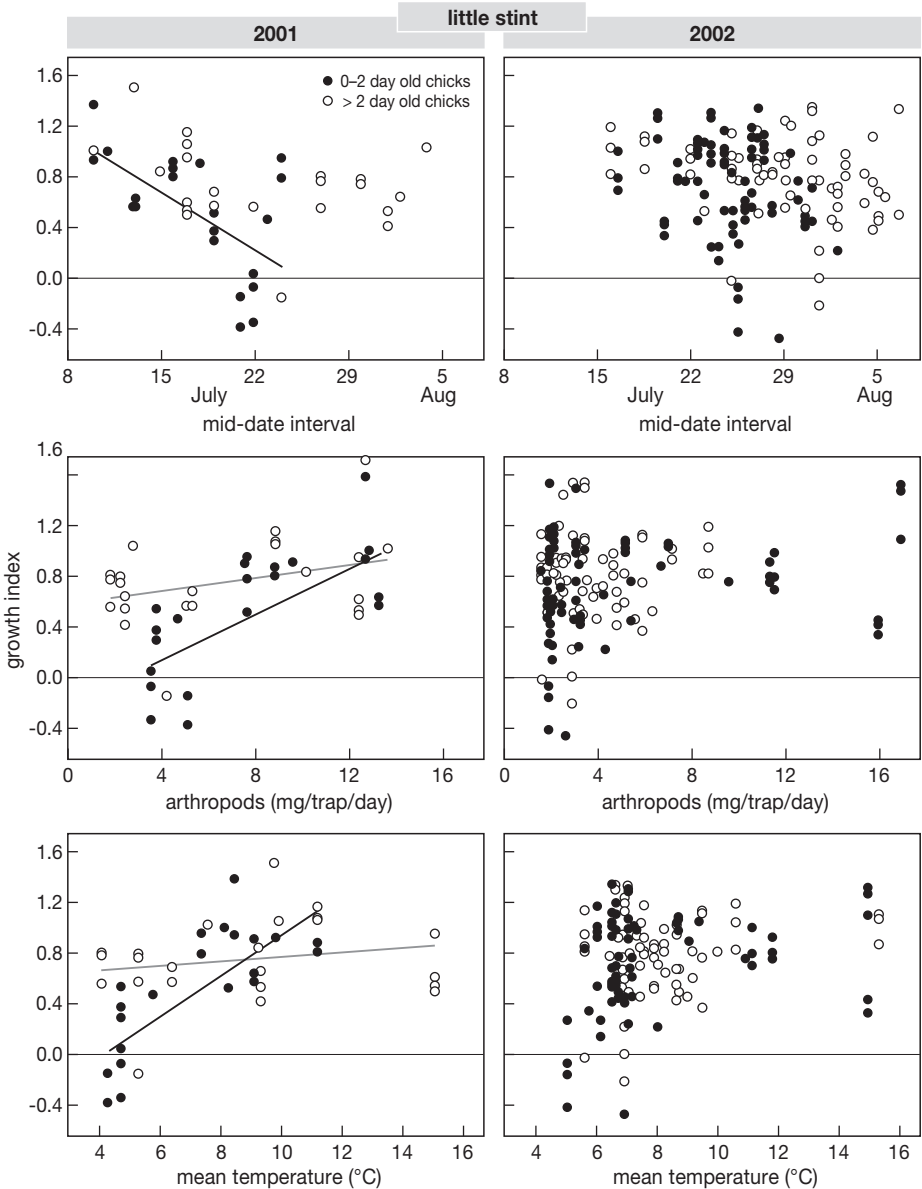


Table 8.2. Results of Linear Mixed Models to analyse the effect of mid-interval date, temperature, wind speed, rain and arthropod mass on growth (growth index) of dunlin chicks. Nest/brood and ring number were entered as random variables. Because of the correlation between the weather-related variables and mid-interval date, these were analysed separately. For every year the effect of mid-interval date was investigated and in separate model the effect of weather and arthropod mass. Models were first run for both age groups combined; if no effect was found separate analyses were run for each age group.

year	N	age group	model	Wald	P	effect	SE
2001	32	all	mid-interval date	11.92	<0.001	-0.0327	0.0080
			age	19.39	<0.001		
			age 0-2 days			0.0000	0.0000
			age > 2 days			0.3171	0.1083
		all	temperature	not significant			
			age 0-2 days	34.40	<0.001	-0.2053	0.035
			age > 2days	13.64	<0.001	0.0665	0.018
		all	wind speed	5.00	0.025	-0.0820	0.0206
			age	23.22	<0.001		
			age 0-2 days			0.0000	0.0000
			age > 2days			0.4104	0.0852
		all	rain	40	<0.001	0.1028	<0.001
			age	5.67	0.017		
			age 0-2 days			0.0000	0.0000
			age > 2days			0.1603	0.0673
		all	arthropod mass	15.91	<0.001	0.0548	0.0110
			age	26.55	<0.001		
			age 0-2 days			0.0000	0.0000
			age > 2days			0.4405	0.0850
		all	wind speed	8.47	0.004	-0.0329	0.0253
			arthropod mass	7.65	0.006	0.0414	0.0143
			age	28.22	<0.001		
			age 0-2 days			0.0000	0.0000
			age > 2days			0.4579	0.0862
2002	15	all	no significant relations				

Growth rate in dunlin

For dunlin data of chicks of one day old and older (age in days) of known age were used to fit the logistic growth curve for body mass. We used the mean mass of fledged juveniles caught at the end of the season as an asymptote (46.4, SD = 2.8, N = 10, Schekkerman et al. 2004). The fitted growth curve resulted in: $\text{mass} = 46.4 / (1 + \exp(-0.2297 * (\text{age} - 7.136)))$ (figure 8.3).

Growth of dunlin chicks in 2001 decreased in the course of the season and was positively related to arthropod mass and negatively to wind speed and rain (figure 8.4, table 8.2). The intercepts of these relations were all different between the age groups, but none showed a different slope. The effect of temperature was not significant, but analysis per age group resulted in a significant negative slope for the youngest chicks, but a positive slope in older chicks (figure 8.3, table 8.2). Tested in combination, growth rate was best explained by a model containing wind speed, arthropod mass and age group (table 8.2). In 2002 no significant relationship of growth rate with any of the variables tested was found in neither young nor old chicks (table 8.2).

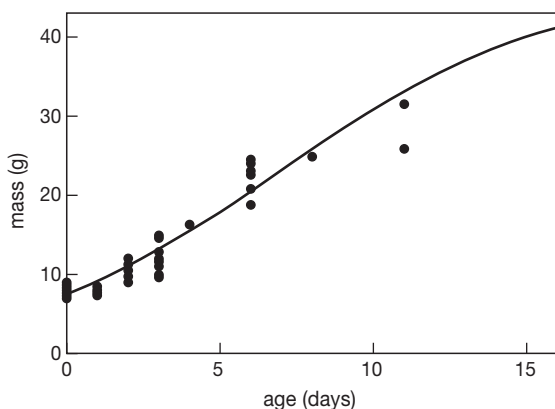


Figure 8.3. The growth rate of dunlin chicks of known age. The data points show individual measurements of chicks, and the curve is the logistic growth function.

Brood survival

In 2001 in both species, the reduction in growth rate with date was paralleled by a declining probability that broods with young chicks (up to c. 4 days) were recaptured or seen again at least two days later (figure 8.5). The probability that a brood of little stint and dunlin chicks was recaptured 2 days after their initial capture decreased significantly with date of birth (little stint: $\chi^2 = 8.07$, $P = 0.005$, $N = 57$; dunlin: $\chi^2 = 3.84$, $P = 0.050$, $N = 18$). Due to predation in 2001 many first clutches of dunlin were depredated and most pairs laid a second clutch. This caused the relatively long laying period and consequentially large spread in hatching dates. Little stints do not relay after nest failure, but have a longer laying period due to their double-clutch mating system (Hildén 1988). In 2002 hatching dates were more synchronised due to a late start of breeding, caused by an extreme late snow melt (chapter 10). In this year for neither species a relationship between brood survival and hatching date was found (little stint: $P > 0.1$, $N = 63$; dunlin: $P > 0.1$, $N = 17$).

Figure 8.4. Growth index over recapture intervals in relation to mid-interval date, arthropod availability, and mean temperature for dunlin in 2001/2002. For the explanation of growth index see text. Lines are regression lines for and are only presented if the explaining variable is significantly related to growth rate (lines for 0-2 days old chicks, dotted lines for chicks > 2 days).

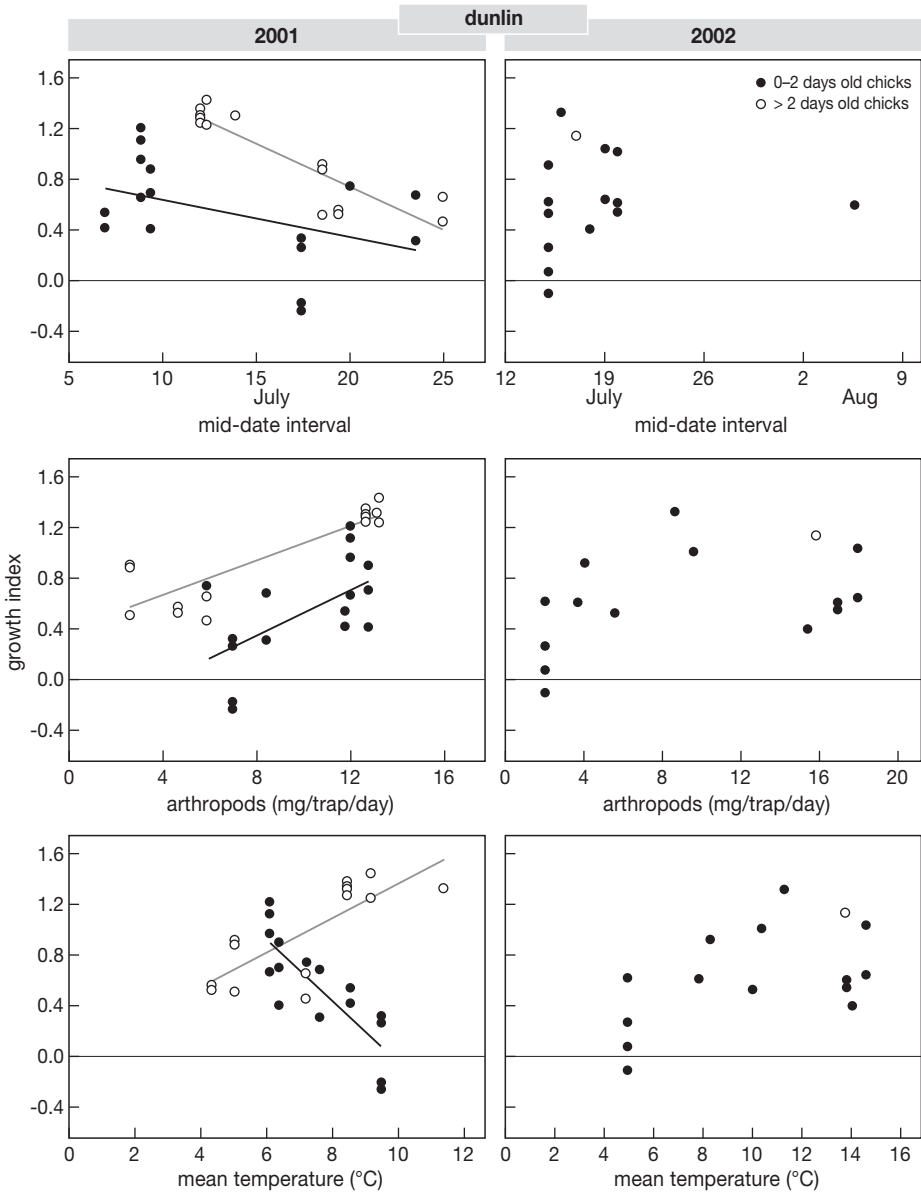
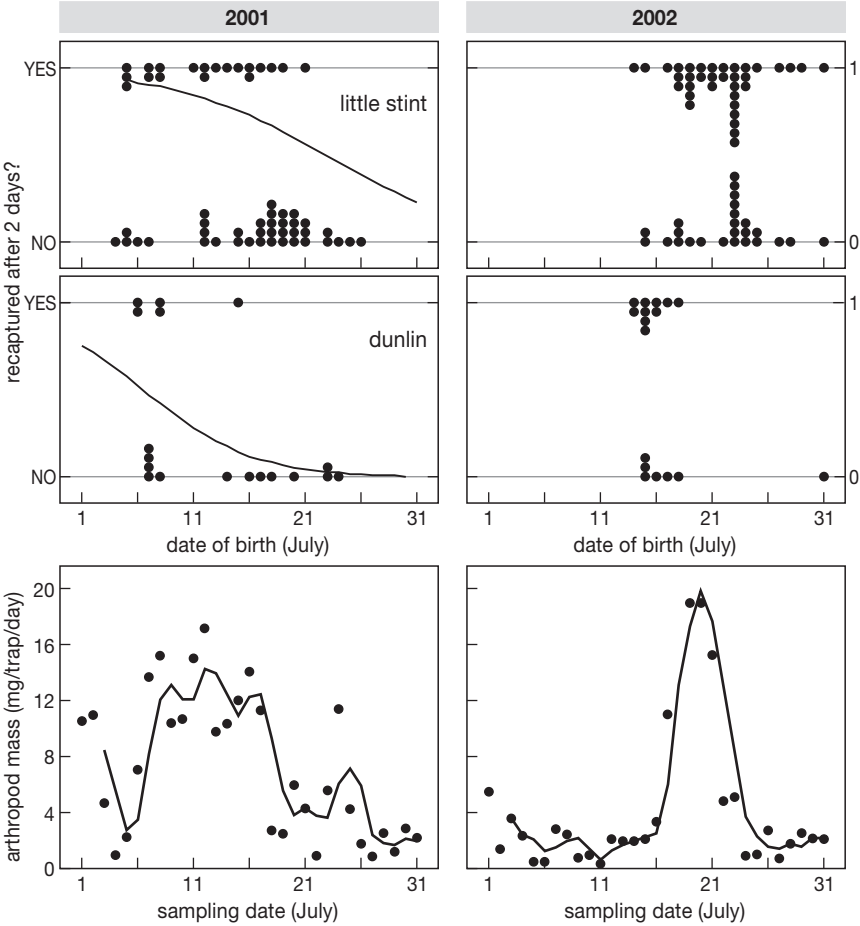


Figure 8.5. Probability of recapturing or resighting broods with small chicks at least two days after ringing for little stint and dunlin in 2001 and 2002 in relation to birth date. Lower two panels represent food abundance (arthropods) as measured in pitfall traps (see chapter 9). The line is a three day running mean.



Discussion

Factors influencing breeding productivity

Although records of the influence of hatching date and weather on chick growth and survival are plentiful in altricial species (Nooker et al. 2005; Arnold et al. 2006; Hart et al. 2006), similar studies in self feeding (precocial) chicks are rare (but see Ruthrauff and McCaffery 2005). So far, similar correlations between season, weather or food and productivity in precocial insect-feeding species have only been demonstrated in wigeon *Anas Penelope* (Gardarsson and Einarsson 1997), Pacific golden plover *Pluvialis apricaria* (Pearce-Higgins and Yalden 2002), curlew sandpiper (Schekkerman et al. 1998b), red knot (Schekkerman et al. 1998b; Schekkerman et al. 2003b), and western sandpiper *Calidris mauri* (Ruthrauff and McCaffery 2005). In chicks that are fed, the influence of weather on chick growth generally works through increased thermoregulatory costs in inclement weather (Ritz et al. 2005) or food abundance (Hart et al. 2006) as well.

Growth of little stint chicks was found to increase with temperature, food abundance and decrease with wind speed in 2001 for both young and old chicks, while the effect of date was only significant in young chicks in 2001. The significant positive effect of rain was contrary to expectation. In dunlin a positive effect of temperature was only found in older chicks, while the increase in growth rate with increasing food abundance, decreasing wind speed and rain was apparent in all chicks. In the absence of shelter on the arctic tundra, it comes as no surprise that wind increases thermoregulatory costs of arctic breeding shorebird chicks (Bakken and Williams 2000).

Because the average arthropod biomass over recapture intervals declined strongly with mid-interval date in 2001, especially after 15 July, chicks of both species grew more slowly as the season progressed. Although the effect of temperature and food on chick growth rate are partly aliased, models with both effects explained additional variation compared with the simple models (table 8.1). In 2002 we found no significant effect of any of the variables tested in neither species. This is in contrast to an earlier report on the same data by Tjørve et al. (in press), who described a significant decrease of growth rate in relation to date in 2002. In that study however, in the analysis every data point was used as an independent value, not correcting for multiple measurements of the same chick or sibling effects, which results in a less conservative test. Using mixed models that do take account of different



levels of variation, the relationship with mid-interval date was significant in 2001 but not in 2002. This could be caused by lack of variation in weather conditions in the chick period in 2002 (figure 8.1). Because of the late snowmelt in 2002, the breeding season was late and condensed, causing breeding attempts to occur highly synchronised. Unlike other years (chapter 9), the food peak was very narrow and most chicks hatched well after it, during a period that showed little variation in weather and arthropod abundance. Days with temperatures below 5°C, when the strongest reductions in growth rate were observed in 2001, rarely occurred in 2002. As a crude estimate of the survival of chicks, the probability for broods that were ringed 2 days or later after ringing to be resighted, showed a decline in course of the season in 2001 (figure 8.4), indicating that the declining arthropod availability affected chick survival. It is consistent that a seasonal decline in survival was not found in 2002.

Because of their smaller size we expected any effect of weather and food on growth rate to be stronger in little stints than in any larger species. In comparison to the growth effect found in little stint and dunlin, the effect of temperature and food availability on growth rate was more pronounced in red knots, breeding in northern Taimyr (Schekkerman et al. 1998b). In this species the relationship was best described using the logarithm of mean daily arthropod mass, with a reduced growth rate (index values < 1) at daily arthropod dry mass values of less than 10 mg/day/trap. The curvilinear shape as apparent in red knots was not found in our study; the logarithm of daily arthropod mass did not provide a better fit than the non-transformed values. The growth index in little stint was on average lower than 1.0 (figure 8.2), indicating that growth was retarded in comparison with other areas or years represented by the general growth curve used as a yardstick (Schekkerman et al. 1998a). In both little stint and dunlin, growth indices dropped below 1 at daily arthropod catches of less than 10-12 mg/day/trap (in 2001, figure 8.2 and 4), similar values to that observed in red knot. The only other study where a relationship between growth rate and food abundance in an arctic species was established, the curlew sandpiper, was based on fewer data points (Schekkerman et al. 1998b). A comparison of the level of food abundance where growth is retarded can not be made directly with curlew sandpiper, as arthropod abundance was not measured in dry mass in that study, but numbers instead. Growth index dropped below 1 at ca 10°C, which corresponded to 9-10 arthropods/day/trap (Schekkerman et al. 1998b).



From own sampling we know that an average arctic arthropod weighs ca. 1.4 mg (chapter 9). Based on this value daily arthropod catches equals 12-14 mg dry mass /day/trap, even exceeding the values in our study.

Because of the differently shaped relationship, comparisons of the slopes, representing the strength of the effect of weather and food, cannot be carried out. Naturally, the data from these three studies were collected at different locations, latitudes and years, but the resulting threshold level for growth all seem to be within the same order of magnitude. Given the large year to year variation in the relationship between weather and food and chick growth, testing the hypothesis that an effect of weather or food is expressed stronger in smaller species, would require a study on a range of differently sized shorebird species at the same site in the same year.

Annual variation in opportunities for successful reproduction

The main factor affecting hatching success is predation on eggs. After hatching, predation on chicks can still strongly reduce the number of fledged young. In the Siberian arctic lemming abundance is an important, and perhaps conditional, factor determining reproductive success in shorebirds. Although breeding success in shorebirds is not as discrete between good (lemming rich) and bad (lemming poor) years as for instance in brent geese *Branta b. bernicla* (Summers and Underhill 1987; Underhill et al. 1993), some of the variation is explained by lemming abundance (Underhill et al. 1993; Schekkerman et al. 1998b). This means that beneficial conditions for breeding with regard to the effect of predation only occur every few years.

Our results in this study show that chick growth can be highly influenced by weather and food abundance if the chick period coincides with a period of adverse weather, as shorebird chicks do not have reserves to overcome such periods (Norton 1973). A few consecutive days with adverse weather can be sufficient to decimate the number of surviving chicks. In another study (chapter 9), we showed that the timing of the peak in arthropod food is highly variable between years and is not predictable. The way shorebirds apparently deal with this uncertainty is that they start breeding as early as possible, i.e. right after the snow melts (Schekkerman et al. 2003a). For most years this means that they maximise the probability that chicks hatch when food peaks (chapter 9). Whether food will be sufficient, largely depends on the weather variation on a day-to-day time scale. Reproductive success can therefore be severely reduced by adverse weather in the chick period, also in years with low predation pressure. The close correlation between the juvenile percentage on wintering grounds in curlew sandpiper (Schekkerman et al. 1998b) and dunlin (Beale et al. 2006) with temperature during breeding illustrates this.

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Een grillige toendra

De kans dat het steltloperouders lukt om hun eieren uit te broeden en hun jongen vliegvlug te zien worden, wordt door verschillende factoren beïnvloed. Steltloper-eieren en -kuikens zijn een gewilde prooi voor poolvossen, jagers en meeuwen, maar lang niet zo gewild als lemmingen. In jaren met genoeg lemmingen hebben steltlopers daarom niet zo veel te vrezen van poolvossen en andere jagers. Omdat de aantallen lemmingen in Siberië sterke en over grote gebieden synchroon verlopende fluctuaties vertonen, varieert de kans op predatie sterk tussen jaren. Tot voor kort vertoonde de lemmingstand een driejarig cyclisch patroon. Recentelijk loopt de cyclus wat uit de pas, maar er komen nog steeds lemmingrijke en lemmingarme jaren voor, al lopen die niet meer synchroon over heel Siberië.

Maar niet alleen de predatiedruk varieert sterk, ook het weer kan het ene jaar veel gunstiger zijn dan het andere. Op het moment dat de kuikens uitkomen zijn ze afhankelijk van voldoende voedsel en gunstig weer. Omdat ze hun eigen temperatuur niet kunnen reguleren, moeten ze regelmatig bebroed worden. Maar als het weer zo slecht is dat ze snel afkoelen blijft er bijna geen tijd over om voedsel te zoeken. Bovendien zijn er dan ook weinig insecten, hun stapelvoedsel, te vinden. Enkele dagen met lage temperaturen, regen of sneeuwbuien, hetgeen niet ongebruikelijk is in Taimyr, zelfs niet midden in de zomer, kan funest zijn voor kuikens.

In het eerste jaar van onze studie, 2000, waren er geen lemmingen en de meeste nesten werden gepredeerd voordat ze uitkwamen. In 2001 en 2002 kwamen er wel behoorlijk wat nesten uit. Het echte broedsucces meten, in de zin van hoeveel kuikens er vliegvlug worden per ouder(paar) is erg moeilijk bij deze soorten, omdat ze extreem goed gecamoufleerd zijn en je de kuikens, zeker als ze eenmaal wat ouder zijn, niet makkelijk te zien krijgt. Maar in de veronderstelling dat alleen kuikens die goed groeien een goede kans hebben om vliegvlug te worden, hebben we kuikengroei als maat voor broedsucces gebruikt. Als de eieren uitkwamen bezochten we het nest en ringden we de kuikens. Door ze daarna regelmatig terug te vangen als we ze ergens op de toendra tegenkwamen, konden we de groeisnelheid meten. Tegelijkertijd hielden we ook bij hoeveel voedsel er beschikbaar was. Doordat juni in 2001 erg warm was smolt de sneeuw sneller weg dan in 2002. Verder scheen de zon veel minder vaak in 2002 en regende het veel vaker. Het was kortom stabiel maar grijs weer.

Door het grilliger weerpatroon in 2001, met meer pieken en dalen, varieerde het insectenaanbod veel sterker. Dat gold vooral voor de periode waarin de meeste kuikens geboren werden. Als



gevolg daarvan was er in 2001 een duidelijk waarneembaar effect van het weer en de hoeveelheid voedsel op de kuikengroei. Kuikens groeiden slechter in perioden met lage temperaturen en weinig voedsel dan in warmere perioden. Bovendien was er een verband met de datum: de vroegst geboren kuikens groeiden het beste. Ook bleek dat de kans dat we een familie met kuikens überhaupt nog een keer terugzagen nadat we de jongen in het nest geringd hadden, sterk af te nemen in de loop van het seizoen. Een aanwijzing dat laat geboren kuikens minder goed overleefden.

Ondanks dat we in 2002 veel meer kuikens konden meten en de dataset dus veel groter was, vonden we deze verbanden in dat jaar niet. De verklaring daarvoor ligt in het feit dat door de extreem late sneeuwsmeelt het hele broedseizoen in elkaar geschoven was: alle nesten waren binnen een week gelegd! In andere jaren neemt dat vaak enkele weken in beslag. Daardoor kwamen de kuikens allemaal in dezelfde periode uit en hadden hetzelfde weer te verduren. Er zat dus veel minder variatie in de meetserie. Slechts deze twee jaren laten al zien dat de kans op een succesvol broedjaar dus enorm kan variëren. Dit wordt ook goed geïllustreerd door het feit dat het aandeel jonge krombekstrandlopers dat zich tussen de volwassen dieren bevindt in Zuid-Afrika, een belangrijke overwinteringsplek voor deze soort, precies de lemmingcyclus volgt. Maar dat is nog maar een deel van het verhaal. Als je namelijk rekening houdt met de lemmingcyclus blijkt het aandeel jonge vogels (en dus het broedsucces) ook nauw samen te hangen met de temperatuur in het broedgebied in de voor kuikens gemiddeld belangrijkste periode, de eerste twee weken van juli.

Chapter 9



Ingrid Tulp

Hans Schekkerman

Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation

Arctic (in press)

Of all climatic zones on earth, arctic areas have experienced the greatest climate change in recent decades. Predicted changes, including a continuing rise in temperature and precipitation and a reduction in snow cover, are expected to have a large impact on arctic life. Large numbers of birds breed on the arctic tundra, many of which, such as shorebirds and passerines, feed on arthropods. Their chicks depend on a short insect population outburst characteristic of arctic areas. To predict the consequences of climate change for reproduction in these birds, insight into arthropod phenology is essential. We investigated weather-related and seasonal patterns in abundance of surface-active arthropods during four years in the tundra of Taimyr, Siberia. The resulting statistical models were used to hindcast arthropod abundance on the basis of a 33-year weather dataset collected in the same area. Daily insect abundance was correlated closely with date, temperature, and, in some years, with wind and precipitation. An additional correlation with the number of degree-days accumulated after June 1 suggests that the pool of potential arthropod recruits is depleted in the course of the summer. The amplitude of short-term weather-induced variation was as large as the seasonal effect. The hindcasted dates of peak arthropod abundance advanced by 7 days between 1973 and 2003. The timing of the period during which birds have a reasonable probability of finding enough food to grow changed as well: dates with the highest probabilities have also advanced. At the same time the overall length of the period with probabilities of finding enough food have remained unchanged. This results in an advancement of the optimal breeding date for breeding birds. To be able to track this advancement, the start of breeding in arctic shorebirds and passerines must shift accordingly, which could affect the entire migratory schedule. Because our analyses are based on one arctic site only we can not conclude that this is a general pattern for the entire Arctic. To investigate the generality of this pattern, our approach should be applied at other sites too.

Introduction

Due to global warming, the permanent ice cover at the North Pole is melting faster than hitherto expected (McBean 2005; Meehl et al. 2005). According to the Arctic Climate Impact Assessment (McBean 2005), sea ice cover has decreased by 15 to 20% in the past 30 years. Arctic tundras form the northern fringes of the continents bordering the arctic seas. Given the great influence of sea ice on the climate in arctic areas, arctic tundra is one of the terrestrial ecosystems likely to be highly vulnerable to climate change. The annual average temperature has increased at almost twice the rate in the Arctic compared to that in the rest of the world (Callaghan et al. 2005). Generally, vegetation types, snow and weather regimes are expected to show extensive changes, and these changes will be more pronounced in the Arctic than at temperate latitudes (Callaghan et al. 2005). Climate models predict that temperatures will increase (more so in winter than in summer), precipitation will increase and the duration of snow cover will decrease (Kattsov and Källen 2005; McBean 2005).

Arctic tundras are the breeding grounds for a great number of migratory birds that spend the boreal winter in temperate or tropical zones. The long daylight period, sufficient food availability, and possibly a general scarcity of parasites, pathogens and predators, allow their offspring to survive and grow rapidly (Carey 1986; Helmers and Gratto-Trevor 1996; Piersma 1997; Lepage et al. 1998; Andreev 1999; Schekkerman et al. 2003). Birds feeding on terrestrial invertebrates, such as shorebirds and passerines (Custer and Pitelka 1978), make up a significant part of arctic landbird communities (Chernov 1985; Troy 1996). The adults of several of these species and the young of most depend mainly on surface-active arthropods for food. Shorebird chicks feed for themselves from their first day of life onwards, and take arthropods from the tundra surface while walking around attended by one or two parents. Passerine chicks remain in the nest for at least the first part of their pre-fledging period and are fed arthropod prey by the parents.

In the Arctic, arthropods are active and lay their eggs in the summer and spend the winter as eggs, larvae, (pre)pupae, or in some cases as inactive adults (Chernov 1978; Danks 1981a; Danks 1981b; Downes 1981). The latter two strategies in particular can result in a highly synchronised emergence of adults in the summer. Development is controlled by cumulative temperature or temperature thresholds in many species (Danks 1999). At the onset of temperature rise and snow melt the first arthropods emerge. After emergence, adult insects of many species devote their time mainly to reproduction and die shortly afterwards. This results in a characteristic short burst of adult arthropod abundance (MacLean and Pitelka 1971).

The predicted increase in winter temperature is likely to result in an increase in alternating periods of melting and freezing in some areas (Callaghan et al. 2005). These freeze-thaw cycles may reduce the winter survival of insects, either by ice-crust formation leading to anoxic conditions, or by loss of cold-hardiness during an early melt period followed by further freezing (Hodkinson et al. 1998; Sinclair et al. 2003; Hodkinson 2005; Turnock and Fields 2005). With increasing summer temperatures, seasonal patterns of emergence may be altered or disrupted, especially in species with highly seasonal life cycles (Hodkinson et al. 1998). Changes in the phenology of summer emergence may affect the life cycles of the arthropods themselves (in either positive or negative ways), but will also affect the seasonal pattern of food availability for birds (and other invertebrate predators), possibly affecting the optimal timing of breeding for these species. Such an effect is expected if the period in which successful breeding is possible is limited by food abundance. Many investigators have pointed out the synchrony of hatching dates of arctic shorebirds and passerines with the

local midsummer peak in insect emergence (Hurd and Pitelka 1954; Holmes 1966a; Holmes 1966b; Schekkerman et al. 1998; Schekkerman et al. 2003; Pearce-Higgins and Yalden 2004). Schekkerman et al. (2003) have shown that growth rate of shorebirds chicks is correlated with short-term variation in surface arthropod availability and this translates into chick survival. Although not yet investigated in arctic areas, similar correlations between arthropod abundance and chick growth have also been demonstrated in passerines (Hart et al. 2006).

Arctic birds may have difficulties adapting to changes in the timing of arthropod availability if they use timing cues or face constraints (e.g. migration, snow melt) that do not match changes in the timing of food availability (Both et al. 2005). Also, migrating birds may be unable to predict at southerly latitudes (characterised by relatively small climatic change) the start of the season thousands of kilometres north. If birds cannot respond to changes in the timing of prey abundance, this may affect their breeding success and population size (Both et al. 2006). Therefore the seasonal pattern of arthropod surface activity is a yardstick against which changes in phenology of animal groups that depend on them can be evaluated (Visser and Both 2005).

In this paper, we describe the variability in arthropod abundance on the tundra surface during summer in relation to date and weather conditions, on both short (within-season) and long (between-year) time scales, based on four years of field data from one site in arctic Siberia. From a 'food for birds' perspective, short-term relationships between arthropod abundance and weather are as important as long-term seasonal patterns and changes therein, because the former greatly affect the predictability of food abundance. Capitalizing on the tight relationships observed between weather, date and arthropod abundance, we use the statistical model derived from the field data to hindcast arthropod abundance using a 33-year weather dataset collected in the same area. The hindcasted yearly abundance curves are then used to investigate interannual variability and time trends that may have occurred in relation to climate change.

Material and methods

Study site

Data were collected during four summers (1996, 2000-2002) at Medusa Bay, 18 km south of Dikson on the Taimyr Peninsula, Siberia (73°20'N 80°30'E). Field seasons ran from early June to mid-August. The 1996 expedition only covered the period 21 June-21 July and will be used for a subset of the analyses only. The commencement of the field period in the other years was planned so that the observations of arthropod abundance started on the date of emergence of the tundra from under the snow. The study area was situated in the arctic tundra subzone (*cf* Chernov 1985). Vegetation consisted of mosses, lichens, grasses and sedges, dwarf willows *Salix polaris*, and various herbs generally not higher than 20 cm, with a substantial proportion (up to 20%) of the soil surface bare. Patches of bare soil consisted of clay patches with scattered stones (polygonal or spotted tundra, Chernov 1985). On slopes and plateaus on tops of hills (up to 50 m above sea level), the vegetation was generally drier, dominated by grasses, lichens and dwarf shrubs. In the marshy areas found in valleys, on the lower parts of slopes, and sometimes on hilltops, extensive meadows of sedges *Carex* spp. predominated. For a more detailed description of the study area see Schekkerman et al. (2004). During the field period there was continuous daylight.

Weather

In 2001 and 2002 air temperature, wind speed, wind direction and precipitation were recorded every 30 minutes at our study site using an automated weather station. Air temperature was recorded at 1 m above ground level in the shade, while wind speed and direction were recorded at 10 m height. Precipitation was measured in mm/day. In 1996 and 2000 the automated weather station was not yet in use and only air temperature was measured in the study area, and stored in a TinyTag datalogger at 30-minute intervals; all other variables (measured at two hourly intervals) were provided by the meteorological station in Dikson, 18 km north of the study site.

Weather data (daily averages of temperature and wind speed) from Dikson for the years 1973-2005 were obtained through the National Oceanic and Atmospheric Administration (NOAA, www.ncdc.noaa.gov). Given the strong effect of sunshine on the activity of arthropods (Danks 2004), temperature measured at ground level with a black sphere may be a better predictor than air temperature. Although we measured black sphere temperatures in 2000-2002, we chose to use air temperature in the analyses, because that was the only temperature variable available for the long-term dataset. Because air temperature and black sphere temperature were closely correlated ($r = 0.94$), this did not strongly influence our results.

Arthropod abundance

The abundance of surface-active arthropods was monitored using pitfall traps. Two lines of five (1996) or ten (other years) white plastic jars (diameter 11 cm, 10 cm deep) were placed along two line transects at intervals of 5-10 m, one in moderately dry polygonal tundra, the other in low-lying relatively wet sedge-dominated marsh tundra, the same tundra types that shorebird broods frequented. The two lines were ca 100 m apart. The pitfalls were filled with 1-2 cm formaldehyde solution (4%) and a drop of detergent to reduce the surface tension. The traps were emptied every evening around 23:00h and samples were sorted and measured immediately or on the next day. Arthropods were sorted into classes or orders (Araneae-spiders, Collembola-springtails, Coleoptera-beetles, Diptera-flies and midges, Hymenoptera-wasps, Crustacea-crustaceans, Acarina-mites), and Diptera and Coleoptera were separated into families if possible. Springtails and mites were excluded from the analysis, because we considered them to be too small to be energetically valuable for shorebird and passerine chicks, and their contribution to the total biomass sampled was small. Body length of each arthropod was measured to 0.5 mm for animals smaller, and to 1 mm for animals larger than 5 mm. Arthropod dry mass was calculated using the length-dry mass relationships given for different orders in Rogers et al. (1977) and Schekkerman (1997). For orders for which no specific relationship could be found, a general relationship for arthropods was used (Rogers et al. 1976).

The method of pitfall trapping used in this study does not measure absolute abundance of arthropods, but rather a combination of their abundance and surface activity. However, for our purpose of measuring season and weather-induced variation in arthropod availability for birds, this method served well. Several studies have shown a positive correlation between growth of arctic shorebird chicks and arthropod catches in 5-10 pitfalls. Schekkerman et al. (2003) found that this correlation remained after effects of temperature, wind and rainfall on the growth rate of red knot *Calidris canutus* chicks had been controlled for statistically. Conversely, including weather variables did not improve the fit of a model that already contained the number of arthropods caught in 5 pitfalls. This result is only expected if

food availability for chicks is indeed reduced on days with poor pitfall catches. We found similar correlations between pitfall catches and growth rate of chicks of dunlin *Calidris alpina* and little stint *Calidris minuta* at our study site during this study (chapter 8). In cold weather, total abundance of arthropods may be the same as on warmer days but they are inactive and likely to be harder to find by chicks. Although pitfall traps only catch crawling and low-flying insects, this is not a problem given the relative scarcity of high-flying insects in our study area and the fact that shorebird chicks only feed on the ground. In a comparative study in which we used modified (Malaise) traps equipped with vertical screens to catch insects in flight on top of pitfalls, there was little difference in species composition and catch magnitude made by pitfall traps only (Tulp et al. 1998). It might be argued that a sample size of ten pitfall traps is small, but because the day to day variation in numbers caught is so large, variations within pitfall traps is small compared to that and will not disturb patterns in effects of weather and season on arthropod abundance.

Statistical analyses

Log-linear regression (McCullagh and Nelder 1989) was used to analyse the effects of season and weather variables on arthropod availability. To allow for overdispersion in the abundance data, a dispersion parameter was estimated in these regressions. Because size distributions of arthropods did not show a normal distribution, log-linear regression models were also used for the analyses of body size patterns. Variables tested in models to describe the arthropod abundance included: date, mean temperature, cumulative mean temperature (accumulated mean daily temperature since the day of snow melt, treating subzero temperatures as 0 since arthropod activity does not vary once temperatures drop to 0°C or below), mean wind speed, quadratic terms of the four preceding parameters (to allow for nonlinear relationships), the occurrence of precipitation (absent/present on the sampling day) and the amount of precipitation (mm/day).

The models were built starting with an empty model and testing weather variables after entering date and date² (to allow for a curvilinear pattern). To test the independence of date and weather effects, weather variables were also entered first after which date and date² were added to the model.

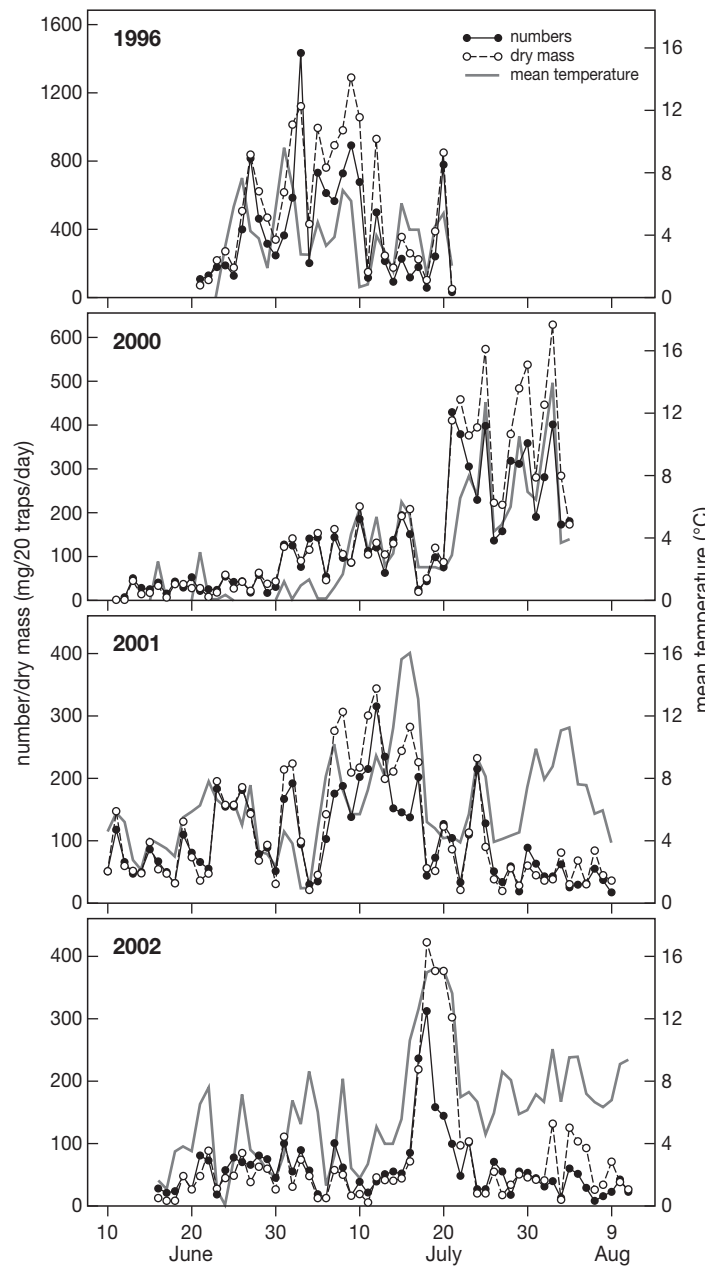
We also considered the possibility that each summer the stock of arthropod larvae, (pre)pupae or imagines that could potentially emerge on the surface becomes depleted. The number of larvae reaching an adequate developmental stage at the end of the previous summer determines this stock. Because of the clear positive effect of temperature on arthropod surface activity and emergence, the cumulative temperature since the date of snow melt is correlated with the number of arthropods already emerged since that date (Hodkinson et al. 1996). Therefore, depletion of this stock of potential recruits will become apparent in a negative effect of cumulative temperature on surface arthropod activity after current weather and date have been statistically accounted for. If the possible effect of depletion is tested in single-year analyses, depletion effects become confounded with the seasonal pattern; the effects of date and depletion can therefore only be distinguished in a multi-year analysis.

To test for differences in phenology between the two habitats sampled we used a log-linear model with dry mass in the two series as the dependent variable and date and date² as predictor variables. If interaction terms date.habitat or date².habitat were significant, the phenology was considered to be different in the two habitats.

Table 9.1. Analysis of seasonal trend in total dry mass of arthropods (mg per 20 traps per day) including weather variables at Medusa Bay in 1996, 2000, 2001 and 2002. The null model includes the constant only, the final model includes all significant parameters shown. The parameters tested included: date, date² (daynr since 1 June, together describing a parabolic curve), mean temperature (in °C), mean cumulative temperature since 1 June, mean wind speed (wind in ms⁻¹) plus quadratic terms and precipitation (in mm per day). In all cases precipitation gave a better fit as a continuous variable than as a categorical variable. If date² was significant but date was not, both were included in the model.

year	model	df	change in deviance	P	coefficient	SE
1996	constant				-1.0600	2.1400
	null model	30	8936.0			
	final model	3	3751.0			
	date	1	0.7	0.953	0.4430	0.1210
	date ²	1	2931.0	<0.001	-0.0063	0.0017
	precipitation	1	820.0	0.050	0.0566	0.0259
2000	constant				2.0030	0.5960
	null model	53	8056.9			
	final model	5	7210.2			
	date	1	5713.8	<0.001	0.1239	0.0253
	date ²	1	203.6	0.001	-0.0011	0.0003
	temperature	1	770.3	<0.001	0.1118	0.0160
	wind	1	415.1	<0.001	-0.0974	0.0276
	precipitation	1	107.5	0.015	-0.9500	0.4100
2001	constant				1.9280	0.4560
	null model	60	3831.0			
	final model	5	2593.0			
	date	1	51.8	<0.001	0.1144	0.0213
	date ²	1	1436.8	<0.001	-0.0016	0.0003
	temperature	1	687.0	<0.001	0.2716	0.0697
	temperature ²	1	181.0	0.006	-0.0102	0.0037
	precipitation	1	236.2	0.002	-0.1386	0.0466
2002	constant				3.0820	0.7060
	null model	54	4159.0			
	final model	4	3285.3			
	date	1	271.4	<0.001	0.0201	0.0342
	date ²	1	645.2	<0.001	-0.0002	0.0004
	temperature	1	2263.9	<0.001	0.0095	0.0788
	temperature ²	1	104.9	0.016	0.0099	0.0040

Figure 9.1. Seasonal changes in numbers and dry mass of arthropods and mean air temperature in 1996 and 2000-2002.



Results

Seasonal and weather-related variation in surface-active arthropod abundance

The two habitats generally yielded the same patterns, although in most years biomass was slightly larger in the wet series. In 1996 and 2000 phenologies were similar in the two trap lines, but in 2001 arthropod abundance peaked two days earlier in the wet series (date.habitat $P = 0.651$, date.habitat² $P = 0.006$) while in 2002 arthropod abundance peaked five days later in the wet series, date.habitat $P = 0.463$, date.habitat² $P = 0.028$). The correlation between the daily catches in the two transects was high (1996: $r = 0.79$, 2000: $r = 0.84$, 2001, $r = 0.63$, 2002: $r = 0.77$). Because of the similar patterns found in both series, dry mass values are combined throughout the following analyses.

The seasonal pattern of total dry mass of arthropods caught in pitfall traps showed a maximum in July in three of the four sampling years (figure 9.1). In 2000, surface arthropod biomass continued to increase until the end of the study period in August. The day-to-day variations were explained largely by weather conditions. As date and weather are partly correlated it is difficult to distinguish between these effects. After adding date + date², weather variables (precipitation in 1996; temperature and wind speed in 2000; temperature, temperature² and precipitation in 2001 and temperature and temperature² in 2002) significantly improved the models that described patterns in total dry mass (table 9.1). Total explained deviances varied between years from 42% to 89%. The lower explanatory power of the model for 1996 is caused by the shorter time series and smaller variation in weather data. In three out of four years entering date+date² after the weather variables instead of before resulted in the same set of significant variables. Only in 2002 date and date² were no longer significant. Hence in most years there was both a unimodal seasonal pattern with a midsummer maximum, and additional variation caused by weather. The amplitude of this short-term variation was as large as that of the seasonal effect (figure 9.1).

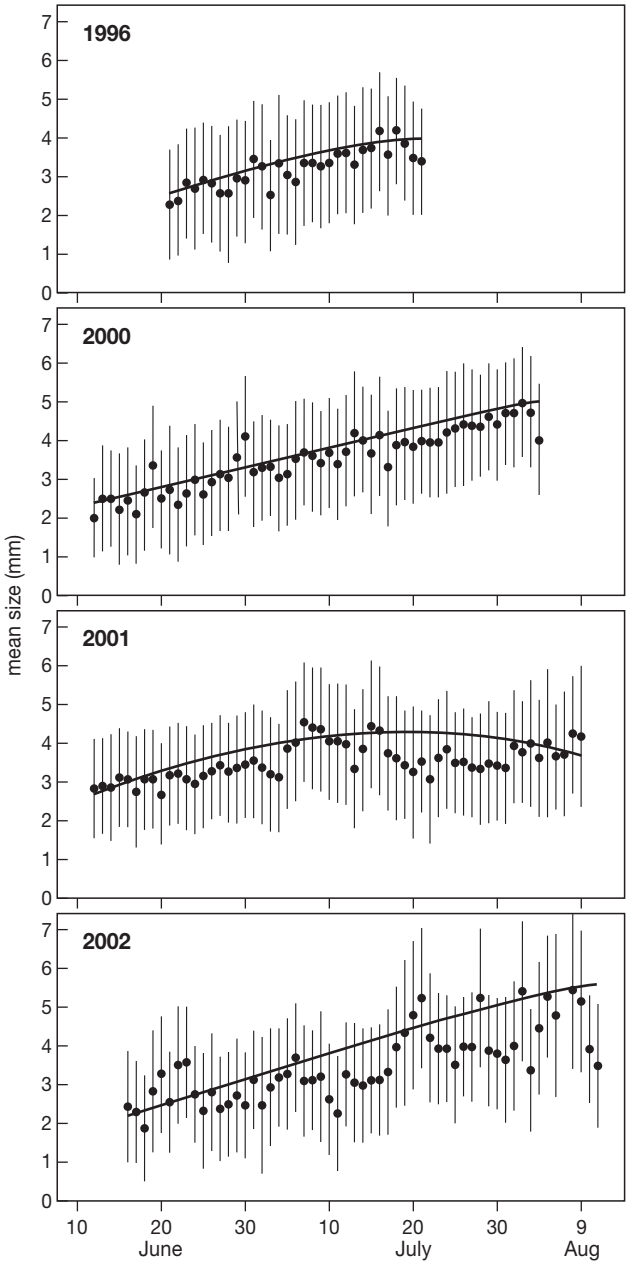
Seasonal variation in size of arthropods

In all years, average body length of arthropods increased with season (figure 9.2, date and date², $P < 0.01$ for all years). Because the body length of insects that have reached their adult phase usually remains stable, the seasonal cline in size must be caused by a trend in the size of emerging arthropods, i.e. small individuals or species emerging earlier than larger ones. Because the various insect families showed relatively small within-group variation in size, the main cause of variation was the phenology of different families. The change in average size is explained predominantly by the emergence of the largest-sized family, crane-flies Tipulidae (Diptera, figure 9.3). Because of their slow locomotion, large size and partial winglessness, tipulids are likely to be an important prey for chicks (Holmes and Pitelka 1968; Pearce-Higgins and Yalden 2004). They emerged in a relatively short and peaked period (figure 9.3). The maximum contribution of crane-flies to total biomass on a day was 86%.

Modelling the peak in arthropod abundance

The measurements on arthropod abundance in relation to weather and date were used to model seasonal patterns in arthropod abundance for a period of 33 years (1973-2005). Over this period, mean temperature in June-August increased significantly in the study area (0.05°C annually). This was the result of a temperature rise in July and August, but not in June (figure 9.4).

Figure 9.2. Mean size (with standard deviation) of arthropods per day in 1996 and 2000-2002. The curves represent the fitted loglinear regression lines.



Data from all four years were used to fit one model describing arthropod biomass with the same variables as used in the analysis for separate years, including year as an extra factor, but excluding precipitation, because data were not available for the 33 year period. Year, date (plus quadratic term), temperature, cumulative temperature (plus quadratic term) and wind all significantly contributed to the model (table 9.2) and together explained 74% of the total deviance. Restricting this analysis to tipulids yielded a similar model but without wind and the cumulative effect of temperature and explained 54% of the deviance.

Figure 9.3. Dry mass caught in the pitfall traps for tipulids and all other groups (non-tipulid) separately.

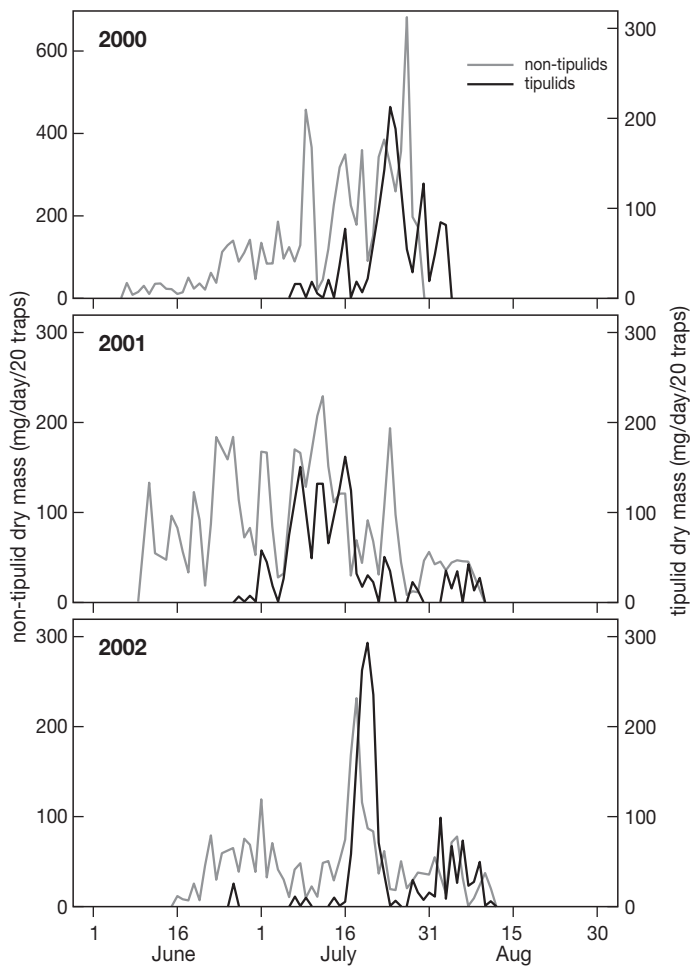


Table 9.2. Results of loglinear regression of weather and seasonal variables on arthropod dry mass, used to model arthropod abundance in 1973-2005. The null model includes the constant only; the final model includes all significant parameters. The parameters tested included: date, temperature (in °C), cumulative temperature since 1 June, wind speed (wind in ms⁻¹) plus all quadratic terms.

response variable	model	change in deviance	df	P	coefficient	SE
total dry mass/ 20 traps/day	null model	43956	200			
	final model	32328	6			
	year	19708	3	<0.001		
	1996				0	0
	2000				-1.317	0.129
	2001				-1.770	0.303
	2002				-2.197	0.195
	constant				4.942	0.576
	date	2051	1	<0.001	0.0320	0.0298
	date ²	2044	1	<0.001	-0.000399	0.000332
	temperature	7486	1	<0.001	0.1306	0.0133
	cum temperature	253	1	0.043	0.00816	0.00536
	cum temperature ²	535	1	0.003	-0.00002710	0.00000944
	wind speed	249	1	0.044	-0.0383	0.0191

Figure 9.4. Mean temperature in June, July and August in the period 1973-2005. The line is the linear regression of mean temperature in the three months ($F_{1,31} = 7.8$, $P = 0.008$).

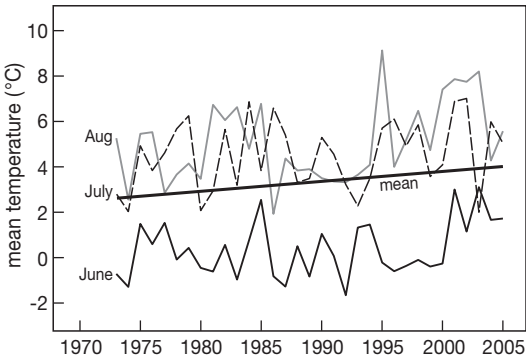
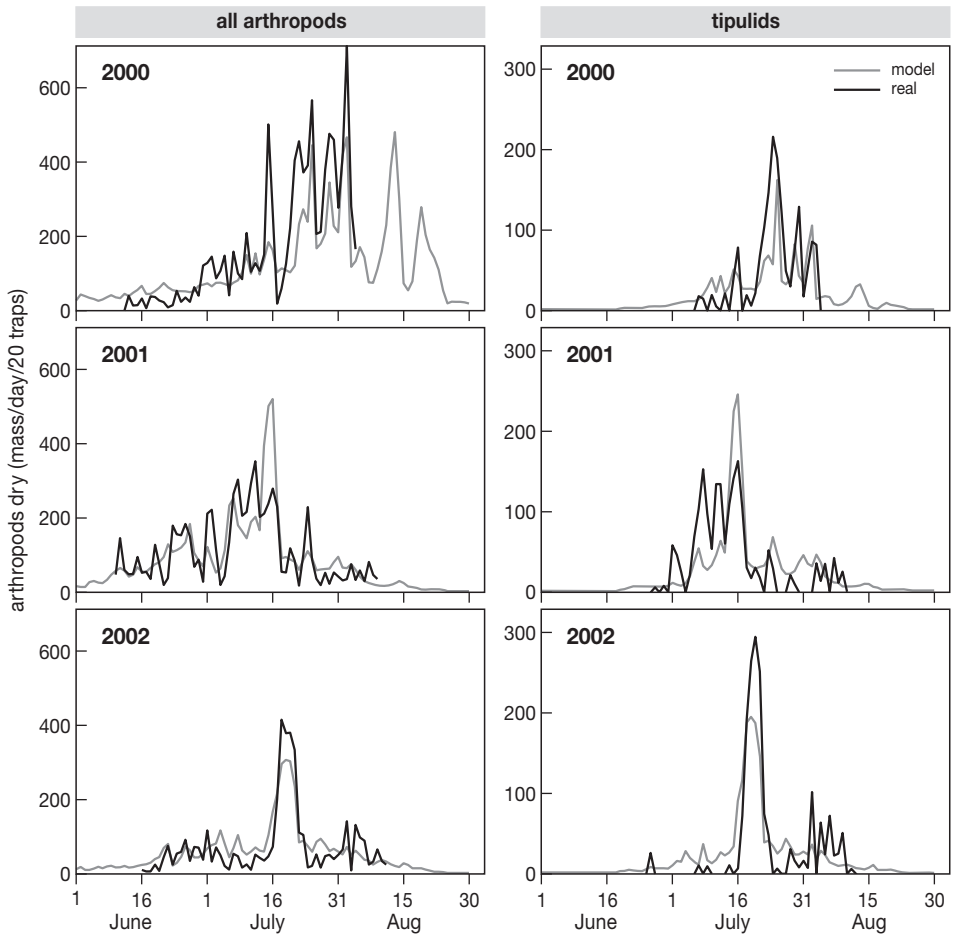


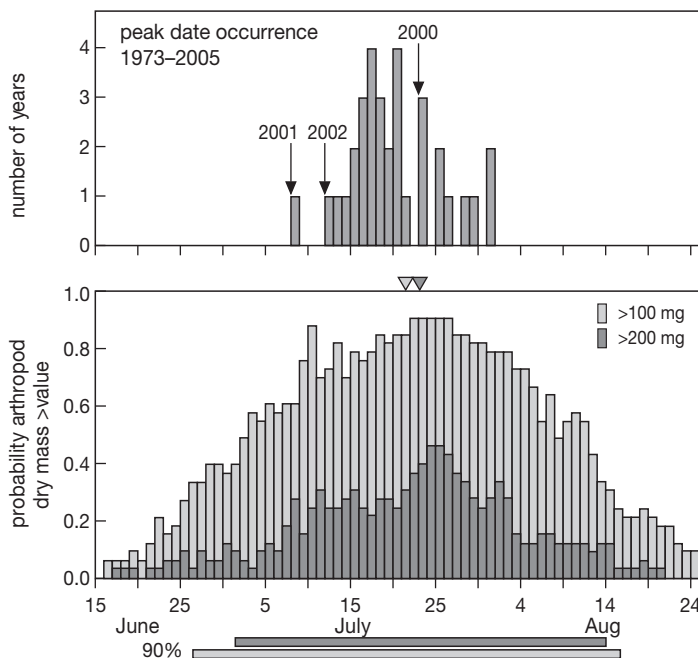
Figure 9.5. Comparisons between model predictions and actual dry mass caught in the pitfall traps in 2000, 2001 and 2002. Data for 1996 are not presented here, because the field season was not complete. Correlations between model outcomes and measured values: total arthropods: 0.90, 0.70 and 0.90, tipulids: 0.76, 0.72, 0.89 for 2000, 2001 and 2002 respectively.



For the years in which arthropod abundance was measured, the fitted model closely matched the actual values, both for total arthropods and for tipulids only (correlations for all arthropods between 0.70 and 0.90, for tipulids 0.71 and 0.88, figure 9.5). Using this model, we then estimated abundance of arthropods (and tipulids separately) for the years 1973-2005 on the basis of the measured weather data. Because year effects can not be extrapolated outside the sampling period, we used the average of the year effects for the four sampling years in our predictions. The year effect determines variation in overall population level between years, but not the seasonal patterns within years which is our main interest.

Dates of peak occurrence in every year were determined by fitting a 2nd-order polynomial (date + date²) to the predicted arthropod abundance (log-transformed) and calculating the date on which the first derivative of each year model equalled zero. In 1973-2005, peak dates ranged between 8 and 31 July and occurred most often on 17 July and 20 July (both 4 years) (median peak date = 19 July, figure 9.6). Over the 33 year period the peak date advanced by 0.2 (SE = 0.07) days per year on average, resulting in a total advancement of 7 days ($F_{1,31} = 5.75$, $P = 0.02$, $R^2 = 0.16$, figure 9.7). The average deviation of the modelled peak date from the long-term average corrected for the long-term trend was ± 4 days (range 0-10 days).

Figure 9.6. Frequency distribution of predicted peak dates in arthropod abundance (upper graph, bars) in the period 1973-2005. The peak dates for the years 2000, 2001 and 2002 are indicated, 1996 is left out because the field data do not cover the whole period. The lower graph represents the probability that total dry mass caught in pitfall traps exceeds the limit of 100 or 200 mg/day/20 traps in the period 1973-2005. The triangles indicate median dates, the bars the central 90% of the distribution.



For chicks it may be more important that they encounter a food supply sufficient for growth, rather than to hit the actual peak in abundance. Red knot chicks were able to grow normally only when arthropod biomass caught in pitfalls exceeded approximately 200 mg per 20 traps per day and growth was severely retarded when arthropod biomass dropped to levels below 100 mg per 20 traps per day (Schekkerman et al. 2003). Choosing 200 mg as a general approximation of a food situation that allows sufficient growth for chicks, we calculated the probability that this level was reached in the model predictions for each date in the period 1973-2005. This probability seldom exceeded 40% (figure 9.6, lower panel), indicating that even at the height of the insect season, days with adverse feeding conditions are common. The probability that arthropod biomass caught was >100 mg exceeded 50% continuously in the period 10 July to 9 August.

To evaluate possible long-term changes in the timing of the total period with a reasonable probability that birds can find enough food to grow, we analysed probabilities that biomass exceeds 100 or 200 mg/day/20 traps, separately for three consecutive eleven year periods: 1973-1983, 1984-1994, 1995-2005. The general pattern that can be derived from this comparison is that dates with enough food supply for chicks to grow have advanced. For the 200 mg limit the distribution of the first period (1973-1983) differed significantly from the last (1995-2005, Kolgomorov-Smirnov test $\chi^2 = 6.28$, $P = 0.043$) but not from the second, nor was there a difference between the second and the third period. For the 100 mg limit the distributions of the first period differed from that of the last period ($\chi^2 = 8.70$, $P = 0.013$) and the last two periods differed as well ($\chi^2 = 6.28$, $P = 0.043$). The number of days in June, July and August with a probability of a minimum of 100 mg has increased significantly in the 33 years ($F_{1,31} = 16.63$, $P < 0.001$, $R^2 = 0.35$). The length of the season (period between the first and the last date with probabilities that arthropod mass caught exceeds 100 mg) has remained unchanged ($F_{1,31} = 0.42$, $P = 0.52$). Similar results were found when using the 200 mg limit (increase in number of days: $F_{1,31} = 6.44$, $P = 0.016$, $R^2 = 0.17$; length of season: $F_{1,31} = 0.26$, $P = 0.61$).

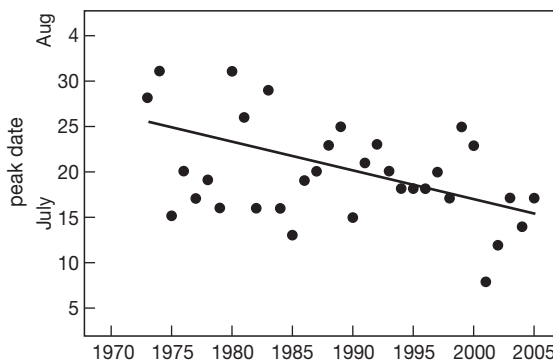
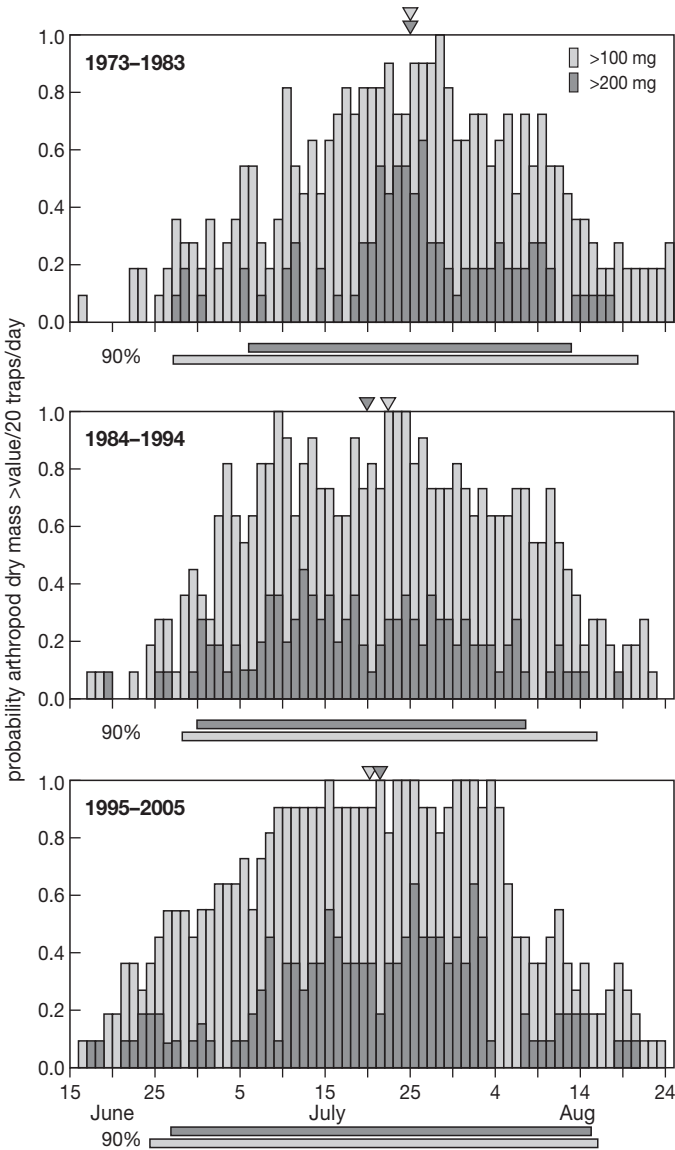


Figure 9.7. Predicted timing of the peak in arthropod abundance in the period 1973-2005.

Figure 9.8. The probability that total dry mass caught in pitfall traps exceeds the limit of 100 and 200 mg/day/20 traps in three periods: 1973-1983, 1984-1994, 1995-2005. The triangles indicate median dates, the bars the central 90% of the distribution.



Discussion

Patterns in arthropod abundance

In this paper we used total catches of arthropods in pitfalls, summed over many taxa, as a measure of food availability to tundra insectivores. Arctic shorebird diets comprise a wide range of arthropod taxa (Holmes and Pitelka 1968) and therefore these totals are likely to provide a useful index of food availability, although bird species may show some differences in the relative share of various arthropod taxa.

We have shown that the variation in the activity and abundance of surface-active tundra arthropods is to a large extent explained by date and weather. Superimposed on a unimodal seasonal pattern, there were strong influences of temperature, wind and precipitation. Similar close correlations with weather were also observed in other studies in both temperate and arctic areas (MacLean and Pitelka 1971; Goulson et al. 2005). The reduction in arthropod mass caught in pitfall traps during cold weather can be explained by mortality, reduced emergence in response to adverse weather, and/or by a reduction in activity. In cold conditions arthropods seek thermally favourable sites and retreat into the moss layer or soil and become less available to birds (Danks 2004).

The significant contribution of cumulative temperature (plus its quadratic term) to the fit of the models already containing date and weather variables indicates that the total number of arthropods ready to emerge can become depleted over the season. This contributes to the peaked seasonal pattern of arthropod availability for birds, and causes food availability to decline well before declining temperatures reach a threshold that would reduce developmental rates and survival of surface-active arthropods.

Weather, date and depletion effects together explained a major part of the total variation in arthropod abundance over our sampling years (table 9.2). This good fit allowed us to hindcast within-year patterns in surface arthropod activity over a long period in the past with some confidence. In the absence of long-term datasets on actual measured arthropod abundances, this exercise provides insights into the variability in timing of food availability for arctic insectivores.

The timing of peaks in arthropod abundance in 2000, 2001 and 2002 fell on 23 July, 8 July and 12 July respectively. Compared to the 33-year period of weather data, 2001 and 2002 were among the years with the earliest peaks in temperature and hence arthropod abundance, but 2000 showed one of the latest peaks (figure 9.6). The occurrence of these extremes within the observation period means that >75% of all years fell within the range captured during our study.

As a consequence of the large variation characteristic of arctic weather (Myers and Pitelka 1979) and its strong effects on arthropod activity, the predictability of the timing of food availability for arctic breeding birds in any single year is rather poor (figure 9.8). In our 33-year set, the average deviation of the modelled peak date from the long-term average corrected for the long-term trend was 4 days.

For chick growth, the exact timing of the peak itself is less important than the occurrence of enough days with sufficient food availability during their growth period. Several consecutive days with adverse weather and low food levels can severely reduce chick survival (Schekkerman et al. 1998; Schekkerman et al. 2003). Our modeling indicated that over the past decades not only the date of peak occurrence, but also the range of dates with a good probability for the birds to find sufficient food for normal growth, have advanced. A potential problem with this second measure of the timing of food availability for birds is that it involves an absolute estimate of arthropod availability (< or > 100 or 200 mg) and

not only a within-year comparison of abundance like in the modeling of peak dates. Because our model can not predict variation between years in overall levels of arthropod abundance (but uses the average of the four observation years), the probability of finding enough food can be predicted with less confidence than the peak date of abundance. However, variation in overall insect abundance between years is more likely to affect the mean level of the calculated probabilities than their distribution over dates. Therefore we interpret the advancement of the probability distributions towards earlier dates as a strong indication that the period with sufficient food availability for reproduction has indeed advanced. The questions remain if and when southern arthropod species will migrate north, and if this migration will affect the total amount of arthropod productivity. Of course, there is no substitute for actual measurements, so we urge researchers to set up long-term monitoring of arthropod abundance patterns in the Arctic (e.g. Hoye et al. 2007), and study the underlying mechanisms generating those patterns. Also the pattern detected in our study area might not be a general one for the Arctic. To evaluate how our site in Taimyr compares to others in this respect, our approach should be applied to other sites as well.

The repercussions of an earlier peak in arthropod abundance for birds

Breeding success in birds depends to a large extent on food availability for the chicks (Lack 1968; Lindholm et al. 1994; Pearce-Higgins and Yalden 2004). In shorebirds, breeding is ideally timed so that chicks hatch during or just before the peak in food availability (Hurd and Pitelka 1954; Holmes 1966b; Holmes 1966a; Schekkerman et al. 1998; Schekkerman et al. 2003). Given the strong seasonality in chick growth and survival (Schekkerman et al. 1998; Tulp and Schekkerman 2001) and the relationship between surface arthropod abundance and chick growth (Schekkerman et al. 2003, chapter 8) the synchronicity of arctic shorebird breeding with the seasonal peak in food supply may be crucial for successful reproduction. In our study period the variation between years in the timing of peak arthropod abundance was very large and even during the peak period, food abundance was highly unpredictable because of strong day to day variations in weather. Shorebirds in our study area and elsewhere in the Arctic seem to deal with this uncertainty by starting to breed as early as possible after the snow melts (Schekkerman et al. 2004; Møltøfte et al. 2007). In this way they maximise the probability that chicks hatch when food peaks. The risk that such strategy would result in the eggs hatching too early is very small, because arthropod abundance starts to build up immediately after snow melt. In years with an early snow melt such as 2000, the period between the start of the first and last nest is much larger than in years with late snow melt as in 2002 (Schekkerman et al. 2004). This is caused by the fact that the last nests were initiated no later than 15 July in all years, indicating that the opportunities for successful reproduction decline or are abruptly truncated later in the season. Studies on breeding phenology in arctic passerines also show that territories are established during snow melt, and that chicks fledge when food is most abundant (Seastedt and MacLean 1979).

Across the period 1973-2005, both the peaks in arthropod abundance and the dates with reasonable probabilities of encountering enough food for chicks have advanced, while the length of the period with sufficient food availability has not changed (figure 9.7). How can birds respond to these changes?

Birds use different cues to determine the onset of breeding. Direct measures of food abundance may not be reliable because gonad development and egg laying take place well before the arthropod peak. If cues that trigger the start of breeding track climate change

in the same way as the insect peak, birds would be able to track these changes. If, however, the cues that are used are not correlated with the timing of the insect peak, an advancement of the period of food availability may result in a reproductive mistiming. The breeding phenology of arctic shorebirds has been shown to be correlated with interannual variation in the timing of snow melt, with a smaller additional effect of temperature during the pre-laying period (Green et al. 1977; Meltofte 1985; Holmgren et al. 2001; Meltofte et al. 2007). An early start of breeding for these ground-nesting birds is only possible if there is enough snow-free area. If the timing of snow melt has advanced less than the seven days advance in the arthropod peak over the past 33 years, the length of the season suitable for breeding would have shortened over this period. Although long-term data on the date of snow melt in the study area are not available, there are several indications that the onset of snow melt has advanced generally in northern Eurasia and other arctic areas (Dye 2002; Stone et al. 2002; Dye and Tucker 2003; Walsh 2005). However, given the high geographical variability therein, long-term local data on snow cover are needed to evaluate whether these two developments keep in pace with each other.

Possibilities to advance timing of breeding by adjusting migration schedules

Most arctic breeding birds are seasonal migrants that winter at great distances from the breeding areas. Because the period between arrival on the breeding grounds and breeding is generally short (Schekkerman et al. 2004; Meltofte et al. 2007), an earlier onset of breeding is possible only if birds arrive earlier. That can be achieved by an earlier departure from the wintering grounds, an increase in migration speed or a shortening of migration distance (Coppack and Both 2002). A long-distance migrant songbird, the pied flycatcher *Ficedula hypoleuca*, tended to arrive from tropical Africa and breed earlier, although insufficiently to track the advancing peak in food supply (Both and Visser 2001; Coppack and Both 2002; Both et al. 2005). This mismatch has already resulted in a significant decrease of the population (Both et al. 2006). Some factor apparently prevents an earlier arrival on the breeding grounds.

The start of spring migration in long-distance migrant birds is induced by an internal clock, synchronised by changes in day length (Gwinner 1996). Although accelerating migration in response to increasing temperatures even in non-breeding areas and along the route has been shown in pied flycatchers (Ahola et al. 2004) and in a study of 20 migrant landbirds (Cotton 2004), changes in the breeding areas may not be perceivable or predictable by birds before their arrival (Visser et al. 2004). This may apply especially to the many species of shorebirds that cover the distance from their intertidal non-breeding and stopover areas to the northern breeding sites in just a few long non-stop flights (Hennigsson and Alerstam 2005). The species that make their final jump from latitudes close to their breeding sites, as some shorebird species along the Pacific Flyway do (B. McCaffery pers. comm.), will be less affected. In the long term, adjustment could take place through selection for earlier arriving birds, although this is likely to occur at a slower rate than the advancement of seasonality (Both and Visser 2001; Coppack and Both 2002; Both et al. 2005). Evidence for the latter mechanism has already been found in long-distance migratory songbirds that are leaving Africa earlier (Jonzen et al. 2006). Such selection is conceivable unless speeding up migration is constrained by dependence on prey that is only available for a limited period of time in specific stopover areas, a phenomenon known for a few shorebird-prey combinations (Zwarts 1990; Zwarts and Blomert 1990; Baker et al. 2004). In theory, time-constrained resource flushes at critical stopovers could also advance in response to climate change if

they are temperature-dependent. This might mitigate some of the costs of changing migration schedules. To date there are very few published studies on long-term trends in timing of arrival and breeding of arctic shorebirds and passerines. Determining whether arctic shorebird populations will be able to adapt to a changing phenology of their food resources and what the effect of such changes will be on reproductive output will require long-term observation programs.

Acknowledgements

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De openingstijden van het arctische restaurant

De arctische zomer duurt maar een paar maanden. De sneeuw begint vroeg in juni te smelten en in het najaar valt de eerste sneeuw (die blijft liggen) al weer in september. Voor veel vogelsoorten die in de Siberische toendra broeden bestaat het voedsel voor een belangrijk deel uit insecten. Die insecten verschijnen echter pas als de sneeuw verdwijnt en bovendien zijn ze maar in een korte en erg gepekte periode beschikbaar. Aangezien kuikens alleen goed kunnen groeien als er voldoende voedsel is, is het dus zaak voor de ouders dat ze op tijd beginnen met broeden. Ze moeten de uitkomst van de eieren eigenlijk zo plannen dat de kuikens precies tijdens die voedselpiek geboren worden of opgroeien.

In drie jaren hebben we het aanbod van insecten dagelijks gemeten met potvallen en geanalyseerd hoe dat afhangt van het seizoen en de weersomstandigheden. De timing van de voedselpiek bleek van jaar tot jaar erg te variëren. Afgezien van hogere aantallen midden in de zomer, bleken dag tot dag schommelingen sterk samen te hangen met temperatuur, wind en regen. Op warme, stille, droge dagen vingen we veel meer insecten dan op koude, winderige dagen met veel regen, vaak wel met een factor vijf verschil. Nu zijn de polen erg gevoelig voor opwarming van de aarde. Effecten van klimaatverandering die tot nu toe zijn waargenomen, komen hier het sterkste en eerst tot uitdrukking. Daarom vroegen we ons af, wat gaat er nu gebeuren als de aarde verder opwarmt en de sneeuw eerder gaat smelten, wat gebeurt er dan met die insectenpiek?

Idealiter onderzoek je dat door over een langere periode (minimaal enkele tientallen jaren) te bekijken hoe die insectenpiek is veranderd. Maar zo'n serie is er niet. Daarom hebben we een trucje gebruikt om het voorkomen van insecten in de afgelopen 30 jaar te reconstrueren. We hebben de verbanden die we vonden in de drie jaar van ons onderzoek gebruikt om aan de hand van weersgegevens te 'voorspellen' wanneer de piek geweest moet zijn in de afgelopen 30 jaar. Dan blijkt dat de timing van die piek gemiddeld genomen steeds vroeger in het jaar valt: een verschuiving van 7 dagen in 30 jaar. Dat lijkt misschien niet veel, maar voor het strakke jaarritme waar veel van de vogels die in de Arctis broeden, mee te maken hebben kan het wel veel uitmaken. De meeste van deze vogels overwinteren op plekken ver weg, waarvandaan ze niet kunnen overzien hoe het met het weer in de Arctis gesteld is. Als de

insectenpiek verder vervroegt, zonder dat de vogels eerder vertrekken uit de overwinteringsgebieden of hun vlucht-schema aanpassen, kan het zijn dat ze op een gegeven moment te laat aankomen.

Als de kuikens pas na de insectenpiek uit het ei komen, is er niet voldoende voedsel meer om goed te kunnen groeien. Tot op zekere hoogte zullen vogelsoorten die van insecten afhankelijk zijn zich kunnen aanpassen, doordat er selectie zal optreden voor vroegbroedende individuen. Die zijn dan in het voordeel vergeleken met de laatkomers en zullen meer nakomelingen krijgen. Maar de vraag is of deze selectie snel genoeg zal zijn om dit soort veranderingen bij te houden.



Chapter 10



General discussion

The different chapters of this thesis discussed a variety of potential selection pressures that may affect the timing of breeding of shorebirds in the Arctic. Below I will first describe how shorebirds timed the breeding in three consecutive seasons in relation to snowmelt, weather and food. In an effort to integrate the results of different chapters, I will here collate all findings regarding selection pressures that affect the breeding season, how their influence may differ as a function of the parental care system and how they differ between parents and chicks. In doing so I also make comparisons between Taimyr and other (especially Nearctic) sites. Occasionally I will use information not previously presented in this thesis. Finally, I will outline how these results can be used to model the effect of arrival date and body condition on reproductive output, in terms of models of migration: the so-called 'terminal reward' function (Ens et al. 1994; Weber et al. 1998; Weber et al. 1999). I will conclude with some ideas of how the change in climate could impact on timing of breeding and based on this summarising discussion, outline what questions remain for a future research agenda.

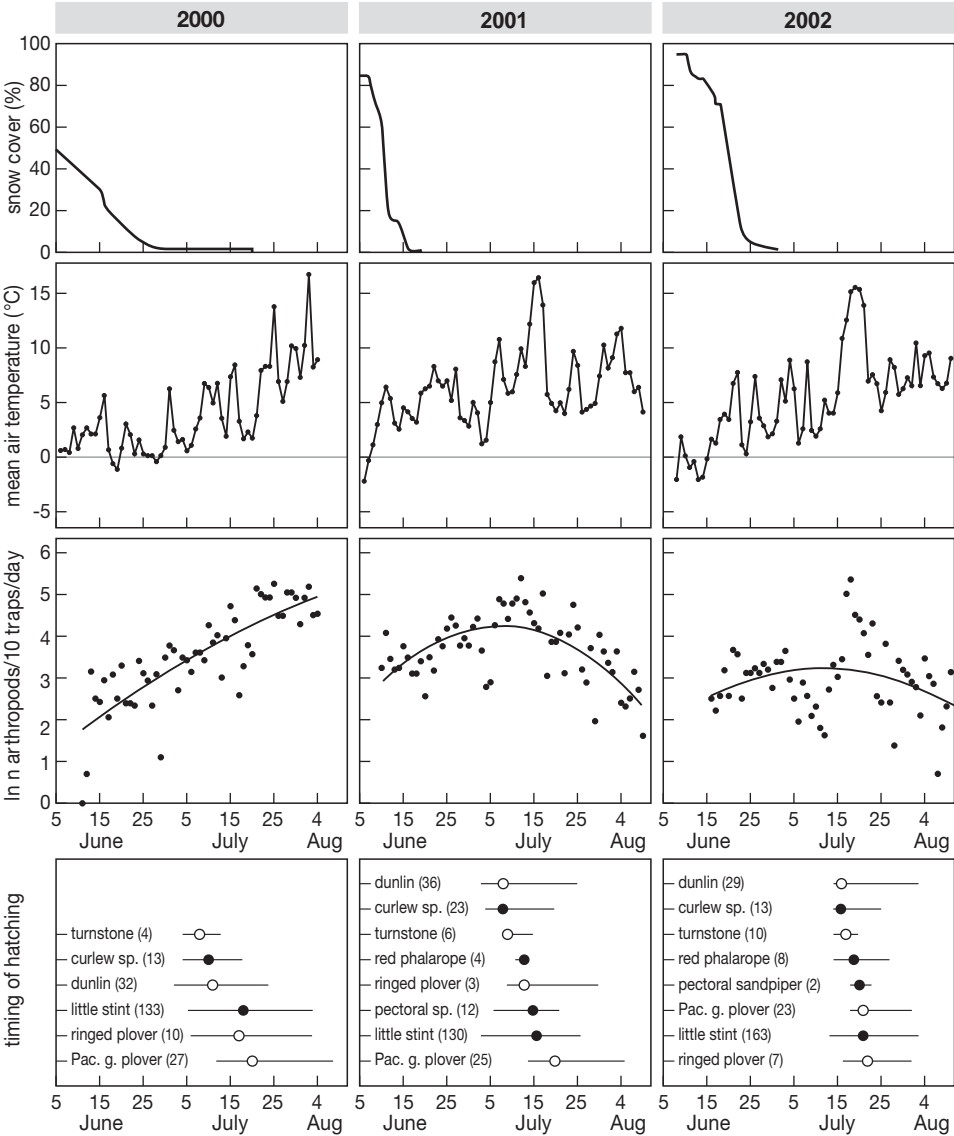
Breeding phenology in Medusa Bay in 2000-2002

Upon their arrival in the tundra in the first two weeks of June, shorebirds generally find the largest part of the tundra surface still covered in snow. However, the year-to-year variation in snow cover in the period when most birds start establishing territories is considerable. Even within the three study years the start of snow melt varied greatly (figure 10.1). For instance, on 5 June 2000 not even half of the study area was snow-covered, while on the same date in 2001 over 80% and in 2002 the whole area was still covered. The rate at which snow disappears also differed between years. In 2001 snow disappeared rapidly due to warm weather, resulting in a practically snow-free tundra by 15 June. In contrast, in 2000 this stage was only reached in the last week of June. In 2002 the snowmelt was the latest ever recorded during studies at Medusa Bay: snow cover was 70% until 18 June.

As the occurrence of surface-active arthropods is highly correlated with weather conditions, the summer peak in abundance also shows variation between years (figure 10.2). Despite this variation, the timing of shorebird breeding was highly similar between 2000 and 2001. In 2002, however, the median laying dates of various species were 4-10 and 2-9 days later than in 2000 and 2001. Furthermore the range between the first and the last nests was much smaller in the late year 2002, with most of the eggs laid within a two week period. In an early year like 2000, this period can be as long as four weeks.

As a result of the relatively late peak in arthropod abundance in 2000 and 2002, most chicks were born when the availability of surface-active arthropod prey was at its maximum. In 2002 chicks grew up on the declining part of the curve. In 2001 numbers of arthropods were already declining by the time that the first chicks hatched. Thus, in three years of study, hatching occurred late relative to the food peak, but an earlier start of breeding was probably not possible because of snow cover. The plovers (ringed plover and Pacific golden plover) generally start breeding later than the sandpipers. The finding that biparental species start breeding earlier than uniparental species (Whitfield and Tomkovich 1996) was only partly confirmed in our studies. When limiting the comparison to the sandpipers, the uniparental curlew sandpiper seems to be the odd one out, starting breeding as one of the earliest. This was exactly the same species that Whitfield & Tomkovich (1996) also identified as being an unusual early breeder for a uniparental species. From all uniparental species this is the only one that nests on dry ridges, a habitat that becomes snow-free relatively early. Not only do uniparental species start breeding later than biparental species, they also arrive later (figure 10.2).

Figure 10.1. Hatching dates (dots: median dates) with range (lines) for shorebird nests (lowest figures), observed directly or deduced from egg flotation or chick measurements at Medusa Bay. Species are ordered by breeding date. Numbers between brackets indicate the number of nests and/or broods on which the distribution is based. Open dots represent biparental breeders, closed dots uniparental breeders. The middle figures show the seasonal patterns in arthropod abundance (on a log scale) and mean temperatures to illustrate the timing of hatching relative to seasonal patterns in food availability and temperature. Snow cover in relation to date is presented in the top figures. Snow cover in relation to date is presented in the top figures.



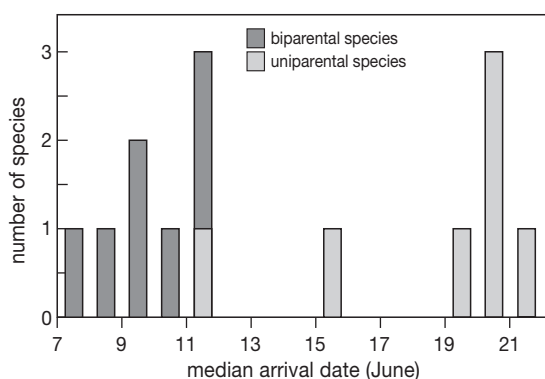


Figure 10.2. Timing of spring migration (median arrival date) in several uniparental and biparental shorebird species in 2001, the only year with good opportunities for migration observations, due to northerly winds, forcing the birds within our view. Daily standard migration counts showed that the timing of arrival differed considerably between the species.

Selection pressures on the timing of reproduction

Arrival in the snow-covered tundra: risk of starvation

Most arctic shorebirds fly to their breeding grounds from distant final spring staging areas (van de Kam et al. 2004). As the weather in the wintering and stopover sites is not likely to be correlated with the snow conditions in the breeding areas (Piersma et al. 1990), the birds have no clues to adjust their arrival to the timing of spring. This is illustrated by the lack of trends in first arrival date of shorebirds in several arctic sites, despite changes in arctic climate, e.g. in the Yukon Kuskowim Delta and Chukotka (Meltotte et al. in press). When the first shorebirds arrive in the high arctic Siberian tundra, the ground is still frozen and largely covered with snow in most years, with scattered snow-free sites, where snow has melted or been blown away. Birds tend to congregate along snow edges where they feed, before they disperse to the breeding territories. Because shorebirds collect the nutrients needed to produce eggs locally (Klaassen et al. 2001; Morrison et al. 2005) and also have to rebuild organs that were reduced before or during the migratory flight, they need food as soon as they arrive. In this period adult birds feed on soil invertebrates such as (tipulid)



larvae and lumbricids along the edges of the melting snowfields; surface-active adult arthropods are hardly available at this time. Although in territorial species competition for the best breeding sites may lead to a selection for early arrival (Kokko 1999), there may also be a severe (survival) cost in years when snow melts late or the tundra surface freezes up for several days after arrival of the birds. Such mortality effects of early arrival in adverse conditions has been documented for barn swallows *Hirundo rustica* (Moller 1994). The fact that there are examples of starvation of shorebirds upon arrival, such as extensive mortality of adult red knots in northern Greenland and Canada in the cold early summers in 1972 and 1974 (Boyd and Piersma 2001) illustrates that this is not merely a hypothetical situation. The leftover reserves that were taken from the wintering grounds and have not been used during migration may only last a couple of days (chapter 2, Morrison et al. 2005).

If birds reach the breeding area in a single flight from a distant stopover site, and laying date is limited by the availability of snow-free habitat, one would expect that arrival date would not be affected by a late snow melt, but that the interval between arrival and laying would be. In our study site we recorded the arrival of previously colour-marked dunlin and analysed whether arrival date was correlated with timing of breeding. Delayed laying in 2002 did coincide with a delayed snow melt, but resightings of colour-marked birds indicate that this did not result in a longer time between arrival and laying. Instead, the birds arrived later and events developed similarly thereafter (Schekkerman et al. 2004). This suggests that dunlins do not fly to their previous year's breeding site directly, but make one or more stops short of their final destination, adjusting their progress across the tundra to local snow conditions.

That such a scenario indeed occurs is also indicated by transect counts made in the snow-free areas of the study plot during the first weeks of the season in 2002 (Schekkerman et al. 2004). Numbers of dunlin counted along the transect were high in the first half of June but initially very few marked birds were seen among them, indicating that the majority were not locally breeding birds. When snowmelt accelerated after mid June, the unmarked birds disappeared from the area and the proportion of marked dunlin rose quickly (figure 10.3). In the Canadian arctic shorebirds have also been observed to stop short of their final destination. This occurred in 1992, for example, when the eruption of a tropical volcano resulted in a very late spring all over the Arctic (Ganter and Boyd 2000). Records at 30 sites showed that arrival was very late compared to other years, followed by a late start of breeding that resulted in an almost complete failure of reproduction for shorebirds and waterfowl. Birds shifted breeding areas or appeared in unusual numbers outside their regular breeding range. The fact that in late springs shorebirds tend to arrive later (Syroechkovski and Lappo 1994; Tomkovich et al. 1994; Tomkovich and Soloviev 1996), provide a strong indication that the final destination is approached in short hops instead of long leaps.

If birds run the risk to starve if they have to wait too long for food becoming available in thawed-out tundra, a prudent final approach to the breeding site is a sensible strategy. But such a strategy also means that 'arrival date' and 'arrival condition' in the sense used in migration models (Weber et al. 1998) have a rather wide geographic definition (ranging over areas several 100 km or more across), and are therefore difficult to measure in the field. This situation is likely to be different for breeding sites that are separated by barriers such as open sea (i.e. Iceland, Greenland). In conclusion, there is a real risk of starvation and as a selective force it will push the optimal arrival date backwards, but arrival date is not as clear-cut a parameter as assumed in migration models.

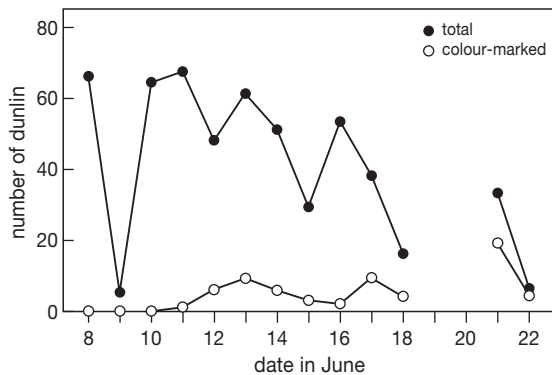


Figure 10.3. Total numbers and numbers of colour-marked dunlin encountered in the snow-free part of the study area during the first two weeks of the 2002 season.

Effects of timing of snow melt and permafrost

Laying date can be constrained by a late snowmelt. Eggs can only be laid once suitable nesting ground has become exposed. But egg laying early in the season is risky: nests in small snow-free patches incur a relatively high predation risk (Byrkjedal 1980). If predators are present at this time of the season they have a reasonably easy job because their search area is limited to the snow-free patches.

An early start of egg laying does not automatically result in an early start of breeding. In shorebirds the four eggs are generally laid in c. four consecutive days, but there are several studies that show a clear correlation between date of first egg laying and the length of the laying period (Tomkovich 1988; Schamel 2000; Meltofte et al. in press). Individuals that start egg laying early took a longer time to complete the clutch, indicating that in early spring either food is limiting or the high costs required for thermoregulation limit the energy to produce the eggs from.

Early in the season the permafrost layer is close to the tundra surface (chapter 3) and eggs are laid only centimetres away from frozen soil. The energy required to warm eggs is significantly greater at low ground temperatures (Cresswell et al. 2004). Despite the fact that the smaller and uniparental species seem to adapt to this situation by constructing better isolated nests (chapter 3), the increased incubation costs caused by the proximity of permafrost may be a factor that causes postponing of egg laying date. Increased incubation cost may be one of the factors that contribute to the general later breeding dates in species with uniparental incubation compared with biparental incubators (Whitfield and Tomkovich 1996). In conclusion, snow cover will push the optimal arrival date backwards, especially in small uniparentals.

Predation risk and lemmings

The risk of predation on the Taimyr peninsula is greatly influenced by lemming abundance, a factor that in Siberia roughly follows a three year cycle (Danell et al. 1999). In years with high lemming densities, predators such as skuas, snowy owls and arctic foxes prefer lemmings over shorebird eggs and chicks, because lemmings are a more profitable prey and easier to find (Angerbjorn et al. 1999). In the year after a lemming peak, the expanded arctic fox population that reproduced very successfully in the peak year will have decimated the lemming population over the winter. In such years arctic foxes are abundant and in the absence of lemmings they mainly feed on eggs and chicks of birds. For this reason breeding

productivity by shorebirds and geese is generally low in lemming low years and high in lemming peak years (Roselaar 1979; Summers 1986; Underhill et al. 1993; Summers et al. 1998; Blomqvist et al. 2002). In the winter lemmings stay under the snow, but as soon as the snow melts and their burrow system falls apart, they will move to their summer burrows. Lemmings become visible on the surface only when snow melt reaches these sites, after the more exposed ridges and watersheds have become snow-free. In springs with rapidly increasing temperatures, lemmings are driven out of their winter sites by snow melt and flooding, while summer burrows in the exposed parts of the tundra are still either frozen shut or flooded with melt water. Only after the soil thaws out the animals can move underground. After two years with extremely low lemming abundance, the numbers of lemmings increased in 2002, though still not very high. The three-year cycle in lemming abundance that has been apparent in Taimyr for several decades was maintained, with an unusually low peak in 2002. During the summer season the probability of predation on shorebird nests was not constant during the summer, but showed a general increase (figure 10.4). Predation started when lemmings, which had been relatively common on the tundra surface for a number of days after their winter haunts in the snow had melted, had moved into the thawed-out summer burrows and became much less available to predators.

Within-season variation in predation risk varies widely across the Arctic (see www.arcticbirds.ru). Both higher and low nest survival of early nests have been described (Reynolds 1987; Tomkovich 1995). Between seasons, however, early seasons generally show better nest survival in most studies (Nol et al. 1997; Sandercock 1998). The problem with the interpretation of these findings is that different mechanisms may be the cause.

In conclusion, predation probability shows a seasonal pattern in some years and in such cases optimal timing of breeding is early. In lemming peak years, however, predation is much less of a problem. In years with rapid snow melt or in years with such low lemming numbers that they are not an interesting prey, the mechanism as described above will not occur. Therefore, effects of snow on the vulnerability to predation interact with the prey situation and the response of predators. As the synchronous lemming cycle is a phenomenon restricted to the Siberian tundra only, this will be less of an issue at other sites because predation pressure is more constant there. Generally Nearctic breeding areas are not characterised by pronounced rodent cycles running synchronously over large areas and overall shorebird breeding success is less variable than in the Russian Arctic (Møltøfte et al. in press, www.arcticbirds.ru).



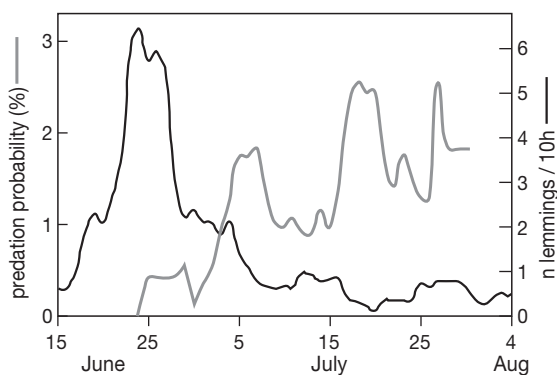


Figure 10.4. Development of daily predation probability (nests predated/nests under observation on each date) for shorebird nests in the summer of 2002, in comparison to development of the number of lemmings observed per 10h in the field. Five-day running means are shown for both predation rate and lemming index.

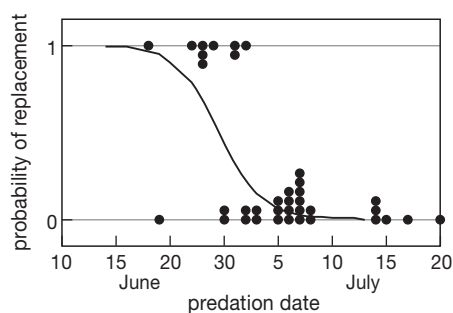


Figure 10.5. Probability of replacement of dunlin nests in relation to predation date in 2000. Every dot represents one nest. The line represents a logistic regression curve: $\text{logit}(p) = 12.46 - 0.507 \cdot \text{predation date}$ (date in June).

Potential for replacement clutches

Several shorebird species that breed in the study area replace their clutches when they are lost to predation. In our area this phenomenon was observed in the biparental species dunlin, ringed plover and Pacific golden plover. The reproductive value of a replacement clutch, however, is likely to decline with progressing date, as the chicks may hatch too late to profit from the midsummer peak in food availability (see below). Delayed egg-laying results in a reduction of time available for re-nesting before the end of the time window that allows a chance of reproductive success. Because a large proportion of the local dunlin population was colour-ringed, replacement clutches of individual birds could be registered. During our studies, replacement clutches occurred mostly in 2000. In that year 9 nests of 17 nests that were depredated before the end of June were replaced, but nests lost after 25 June usually were not (figure 10.5). In 2001 and 2002 there were two and one replacement nests of dunlin, respectively. Because predation will on average occur earlier in clutches that are laid earlier, birds that produced replacement clutches were also the birds that started their first clutch as one of the earliest (Tulp et al. 2000).

Also in other areas late June seems to be a sort of cut-off for probabilities for re-nesting. In a subarctic population of semipalmated sandpipers at La Pérouse Bay, Canada, in late seasons there were no replacements. But in early seasons 47% of those losing nests before 26 June re-nested (Gratto-Trevor 1992). In sanderling on northern Taimyr, in early years one

third of the population may attempt to produce a second clutch as part of the double-clutch breeding system, while in late seasons virtually no second clutches were laid (Tomkovich and Soloviev, 2001). In the Low Arctic, on the Yukon-Kuskokwim Delta, western sandpipers re-nested in all years irrespective of spring timing, but the re-nesting occurred twice as often in the earliest year relative to the latest, and there was a significant linear relationship between median nest initiation date and the proportion of pairs re-nesting (B. McCaffery, unpubl.). In conclusion, re-nesting is only possible in years with a relatively early start of the season and early predation, but offers a second opportunity for at least the biparental species if the first nest fails.

Food for adults

Most arctic breeding shorebirds spend the nonbreeding periods at temperate or tropical shores where they find their food in intertidal areas (e.g. Piersma 1997, van de Kam et al. 2004) and their diets consists of molluscs, polychaetes, crustaceans and other intertidal benthic fauna. In the tundra, most shorebirds seem to rely to a large extent on the same food source: arthropods, notably insects and spiders. Early in the season adult birds feed also on buried insect (Tipulidae) larvae, earthworms (Lumbricidae) and berries, but they switch in diet when arthropod food becomes abundant (Holmes 1966b). The relevance of this buried prey to the adults, especially in early springs, has been investigated in early years in the Canadian Arctic but rarely in the Siberian Arctic (Hurd and Pitelka 1954; Holmes 1966a; Holmes and Pitelka 1968; Holmes 1972). In our study area it seemed that tipulid larvae and earthworms mainly occurred locally in tussocks of moss, something we discovered when observing feeding dunlin, curlew sandpiper and little stint early in the season. This part of arctic shorebird ecology in Taimyr definitely deserves a detailed study in the future. However, judging from the fact that especially after snow has melted away, most shorebirds were actively seen feeding on surface arthropods, we are confident that such arthropods are important for adults also. Little stint clearly demonstrate two different feeding types associated with buried or surface-active prey, categories that are easily distinguished in the field. When they are looking for buried prey they probe with their bills in the soil, often along snow edges, in moss tussocks or in sedge fields. The technique used for feeding on arthropods involves faster pecks directed at the vegetation instead of the soil, with their heads held more horizontally. The transition between these two feeding modes occurred quite abruptly in all three years, as soon as insect catches in our pitfall traps started to increase.

At the start of incubation, the abundance of arthropods is still very low (chapter 9). In the course of the ca 20-25 day incubation period food abundance increases and reaches its maximum around mid July (chapter 9), depending on the weather conditions. After that arthropod abundance declines, a decline that is not merely caused by deteriorating weather, but also by depletion of the stock of arthropods that is ready to emerge (chapter 9). Of course, the pattern in arthropod abundance will only affect adults if food is a limiting factor. The fact that this can be the case at certain periods in some species is illustrated by the body mass dynamics of little stint and curlew sandpiper that show a decline after a few days of inclement weather (chapter 4). Uniparental incubators like these two species have to trade off feeding time against incubation time (chapter 4), and this will increase their sensitivity to the level of food availability for maintaining energy balance (chapter 6). The absence of such a weather effect on body mass in dunlin shows that this species is less vulnerable to bad weather periods and this could well be related to the different parental care system,

allowing each sex up to 12 hours of foraging time each day. The finding that little stints carry extra stores during incubation (chapter 5) is an indication that there is a serious risk that periods with energy imbalance during incubation actually occur. The expected increasing latitudinal gradient in the risk of encountering such periods is indeed reflected in a latitudinal increase in energy reserves in little stints (chapter 5).

So, instead of a timing merely tuned to the chicks' needs resulting in a high reproductive success, optimal timing may additionally be shaped by nutritional shortage early in the egg-laying period or during incubation (Perrins 1970; Drent 2006), and this may apply especially to uniparental species. The proximate force influencing laying date is then the food abundance for the female who has to produce the eggs. While for the chicks an earlier start of breeding would be better, for the parents a later start is better. In these species, energetic stress is higher during incubation, and parental energy requirements may weigh heavier in addition to those of the chicks than in biparental species, resulting in a later optimal time of breeding, closer to the seasonal food peak (Drent 2006).

Food for chicks

In contrast to adults that can take buried prey as well as surface-active prey, chicks, whose bills are not yet fully grown and are not suitable for probing, can only feed on arthropods present at the tundra surface or on aquatic prey in shallow water (Holmes 1966b; Holmes and Pitelka 1968; Holmes 1972; Nettleship 1973; Kistchinski 1982; Schekkerman et al. 2003). When the first chicks are born in the first or second week of July, in many years the abundance of surface-active arthropods reaches its maximum (figure 10.1, chapter 9). During their first week of life the required intake rate is high due to the fact that feeding time is limited, because the chicks need to be brooded a large proportion of the time (Schekkerman et al. 2003). After the first week the energy needs are high because growth rate is fastest in this period (Schekkerman et al. 1998a; Schekkerman et al. 2003). Therefore a large proportion of chicks is in fact born too late: food is already declining again when energy requirements of the growing chicks are highest. The relationships found between chick growth and food abundance illustrate that food is not available *ad libitum*, but that it can reach such low levels that chick growth is actually retarded (Schekkerman et al. 2003, chapter 8).

Spatial variation in food availability might offer opportunities to stretch the period with high food abundance. Differences in microhabitat (sheltering, moistness) may result in variation in the seasonality of arthropod abundance. By adjusting the feeding habitat after the chicks have hatched, some leeway can be gained in the short food season. A study amongst different microhabitats at Cape Sterlegov, northern Taimyr, showed that the seasonal decline of arthropod abundance was steepest in the dry areas and less pronounced in the wetter areas (Tulp et al. 1998). Curlew sandpipers leave their nesting area as soon as chicks hatch and head for the wetter marsh sites (Schekkerman et al. 1998b). At Pronchishev Lake, eastern Taimyr, and Cape Sterlegov the same was observed for grey plovers *Pluvialis squatarola* and turnstones and at Medusa Bay for curlew sandpipers (Schekkerman et al. 1998b; Tulp et al. 1998). Little stints do not wander far away from their nesting sites, but these are generally already situated close to streams and marshes. Examples of movements to wetter habitat by shorebird broods in other parts of the Arctic are also manifold (Holmes 1966a; Parmelee et al. 1968; Nettleship 1973; Ashkenazie and Safriel 1979; Miller 1983).

For an optimal use of the food peak, hatching dates in two of the three years should be earlier than they were. However, the predictability of the timing of the food peak is very poor and the analysis of long-term data indicates that a start as early as possible, i.e. right

after snow melt gives the best chances for a timing that coincides with the food peak (chapter 9). Therefore, from the 'food for chicks' perspective the timing of breeding should be advanced.

Energy needs

Arctic breeding shorebirds spend about twice as much energy during incubation as shorebirds breeding at temperate latitudes (Piersma et al. 2003). It is suggested that these high costs are not caused by the extra energy associated with incubation, but by being active on the cold and windswept tundra with few opportunities for shelter (Piersma et al. 2003). The analysis of DEE during incubation and chick-rearing of little stint and dunlin (chapter 6) showed that although energy expenditure in both phases is equally high, energetic demands will differ because of a difference in time budgets. During incubation the time available for feeding is constrained by the time the eggs need to be brooded. In uniparental breeders the nest can only be left alone for short intervals (leaving only 4-5 hours per day to feed), while biparental breeders each have half the day available for feeding provided that they take equal shares. A way to alleviate the time constraint a little would be the use of a better nest insulation (chapter 3) that would provide more leeway in the time schedule of uniparental species. The scope for such effect, however, is probably limited. During chick-rearing the self-feeding chicks find their own food, but need to be brooded at regular times to maintain their body temperatures. But these brooding bouts take far less time than the eggs require. The rest of the time the parents can feed whenever the chicks feed, but allowing time spent on vigilance. For both groups the time budget in the chick-rearing period leaves more leeway for the parents to feed. In combination with better food conditions and higher air temperatures, the energetic stress is lower than during incubation, but the difference is considerably larger for uniparental than biparental species.

When energetic stress gets so high that the birds' survival or future fitness is at risk, the bird might decide to leave the clutch. Such situations can occur in severe weather circumstances or if adverse weather prolongs, especially late in the season. Nest desertion can also be the result of events such as heavy snow storms (Hildén 1979; Tomkovich et al. 1994), massive passage of reindeer *Rangifer tarandus* (chapter 4) or flooding (Holmes 1966a; Meltofte 1985; Handel and Gill 2001). Although not common, nest desertion did occur in several species in our area, especially in uniparentals: in the three years 25 of 370 little stints, 1 of 83 dunlin, 2 of 79 Pacific golden plover, 1 of 12 red phalarope and 1 of 14 pectoral sandpiper nests under observation were deserted (Tulp et al. 2000; Tulp and Schekkerman 2001; Schekkerman et al. 2004). Desertion of late nests has been reported for many sites (Tomkovich 1988; Gratto-Trevor 1992; Tomkovich et al. 1994; Meltofte 2000; Tomkovich and Soloviev 2001).

Nearly all uniparental incubators in our area showed extra long recesses in their incubation schedule, occurring during or after some periods of particularly inclement weather, lasting up to eight hours (chapter 4). These extra long recesses may indicate that the animal is under energetic stress. Such periods are likely to precede nest desertion. However, many nests in which these long absences were recorded hatched successfully, even if they were in advanced incubation stage.

Energy needs in the different phases of breeding might therefore explain the relatively later start of uniparental species compared to biparental species; they benefit more from an improving food situation and increasing temperatures during incubation. The sharing of incubation duties in biparental species enables an earlier start of breeding.

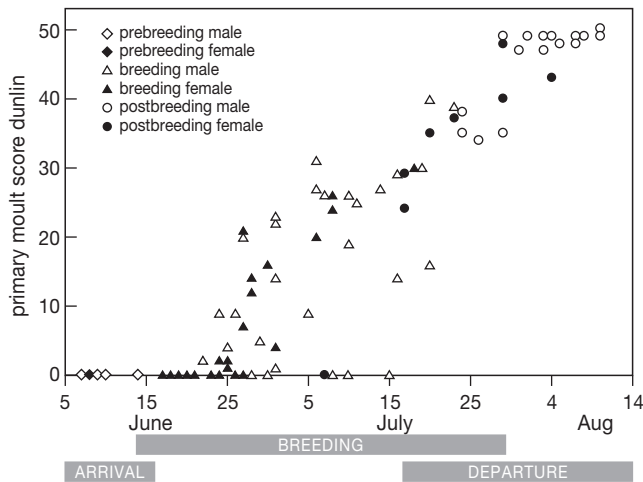


Figure 10.6. Primary moult score of dunlin in relation to catching date.

Competition for food when travelling to wintering area

If there is a benefit of an early departure from the breeding grounds or an early arrival on moulting or migratory stopover sites or the wintering grounds, birds might be in a hurry to leave the tundra in autumn. After the chicks fledge, the parents leave them and migrate to the wintering areas ahead of their young. Early departure by one sex after laying (curlew sandpiper, pectoral sandpiper, phalaropes) or after hatching of the eggs (dunlin, sanderling, red knot), and rapid migration of the remaining parent after fledging of the chicks, point to a premium on leaving the tundra early. There are several indications showing that adults are indeed in a haste to leave the tundra and do not stay longer than necessary.

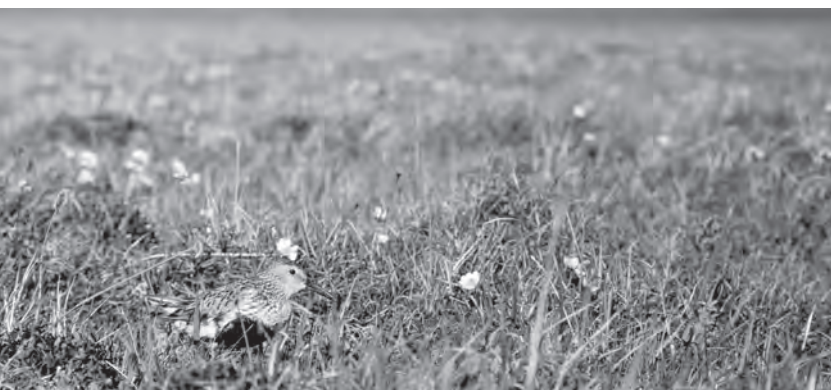
Curlew sandpipers are seen at staging areas in West Europe already from mid July onwards (Bijlsma et al. 2001). These are predominantly males that must have left the tundra shortly after nest completion. Egg laying usually starts in mid June and the period between the first and last nest is laid is two weeks (dates of first and last nest in 2000: 13 June–27 June, 2001: 14 June–28 June, 2002: 23 June–4 July). This time scheme leaves 2 to 4 weeks until the first curlew sandpipers show up in western Europe, indicating that the males will stay in the tundra only for a short period before they leave. In red knots, females leave immediately after hatching and also seem to be in a hurry to leave. In 1994, at Cape Sterlegov, northern Taimyr, many nests of radio-marked birds were depredated, and females left the breeding area within a day (Tulp et al. 1998).

Among tundra breeding shorebirds there are few that commence wing moult while breeding. In our area only dunlin, Pacific golden plover and dotterel were actively moulting their flight feathers while incubating. Apart from catching shorebirds upon arrival (chapter 2), we also caught several species on autumn migration. In dunlin all females and most males that we caught in autumn started migration in a progressed state of wing moult, but just before they had completely finished (figure 10.6). A high proportion of the birds migrated with the outer primary still growing. Apparently they were in such a hurry to start migration and to reach the stopover and wintering areas that they did not wait till they finished their wing moult. In the Nearctic, Holmes (1971) compared moulting schedules of dunlin breeding at two different sites at different latitudes. In dunlin breeding at Yukon Delta breeding

and moult did not overlap in time, but moult is still carried out before autumn migration. At Barrow, 10 degrees further north, dunlin started their wing moult while breeding. So if there is no need to combine moult with breeding, moult is probably postponed till after breeding, but if the summer season is shorter, as is the case in more northerly areas, moult must be combined with breeding in order to be ready before autumn migration.

Depending on the migration strategy during autumn (long continuous flights that require extensive fattening versus short hops that require only short refuelling bouts) shorebirds need time and food for preparation. If they have to put on stores, they need sufficient food at a time when surface-active arthropods start to become depleted. Alternatives in coastal habitats, streams or pools are likely to be of importance at this stage, but are not very common in the arctic tundra range. The strategies chosen probably depends on species size, migration route and local feeding opportunities. Shorebirds in our study area did not accumulate large stores before departing (figure 10.7). Birds travelling from Taimyr can fly mostly along the coast and may find better feeding sites underway, whereas some of the species that breed in Greenland, Canada or Alaska, that have to cross large waters on their way to the south, are known to accumulate large body stores (R.I.G. Morrison, unpubl., M. Klaassen & Å. Lindström pers. comm.). The fact that juveniles from both Nearctic and Palearctic origin do not show high body masses on autumn migration, indicates that also juveniles try to leave the tundra as soon as possible (Lindström 1998; Lindström et al. 2002). When the juveniles have not left before the first permanent snow falls in September, finding food will even become more difficult, and they run the risk of being stuck on the tundra; a situation that has been observed in Canada (Morrison 2006).

Both for adults and juveniles an early departure is apparently the preferred strategy. This can have several reasons. The earlier the start of breeding, the earlier return migration can start. This may reflect a declining food supply in the tundra, but also suggests some advantage of arriving early at autumn staging or moulting sites. Advantages of an early arrival on staging sites may be related to: (1) competition for food (Schneider and Harrington 1981; Boates and Smith 1989; Szekely and Bamberger 1992; Zwarts et al. 1992), (2) competition for best moulting sites in terms of safety or food (van der Have et al. 1984), or (3) trying to stay ahead of the predation wave caused by birds of prey such as peregrines *Falco peregrinus* and merlin *Falco columbarius* migrating southwards (Lank et al. 2003; Ydenberg et al. 2004).



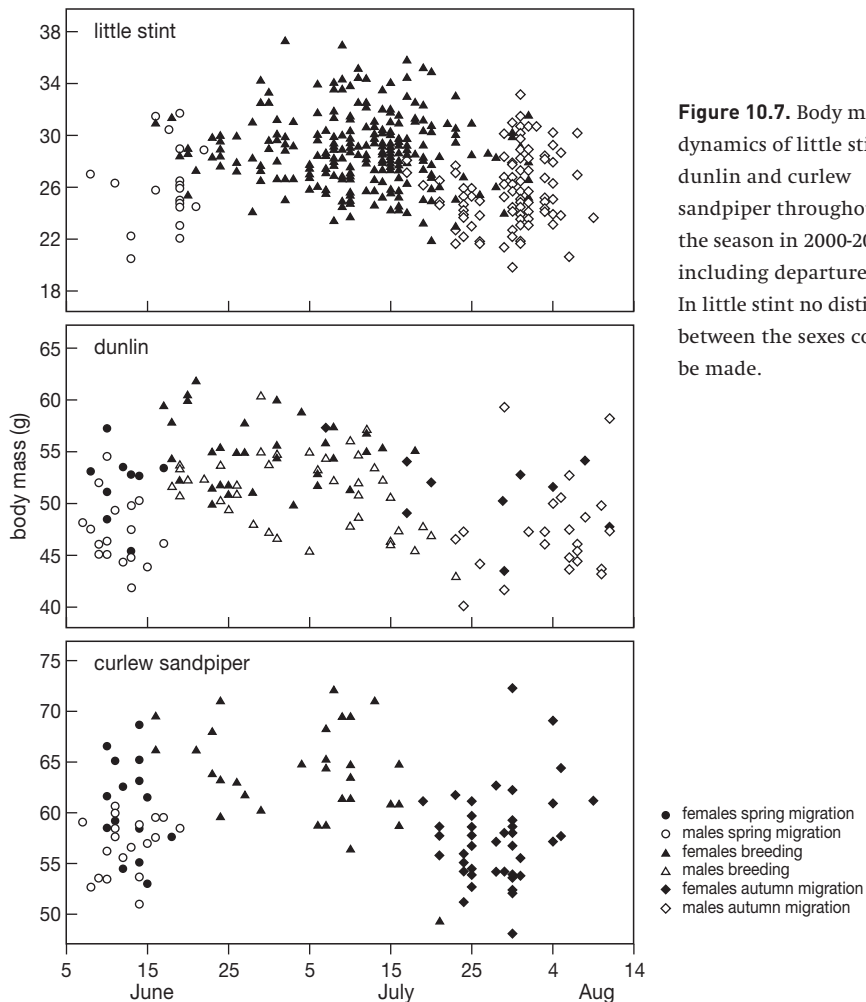


Figure 10.7. Body mass dynamics of little stint, dunlin and curlew sandpiper throughout the season in 2000-2002, including departure. In little stint no distinction between the sexes could be made.

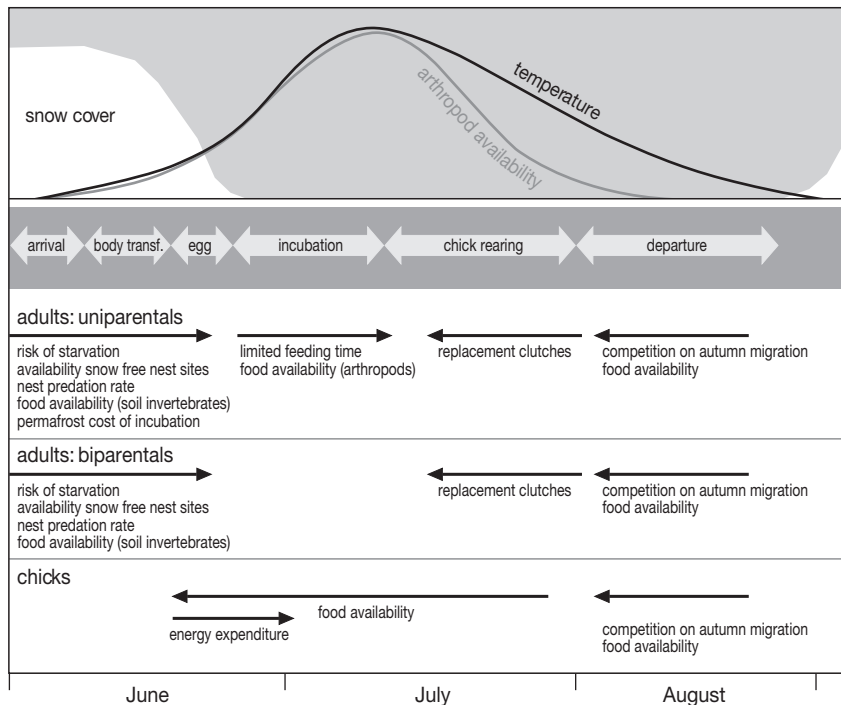
Timing of breeding and parental care system

In different stages of the breeding cycle, different selective forces seem to operate that work in different directions for adults and chicks (figure 10.8). During early spring the snow cover and food availability forces the starting date further into the season, while for the feeding condition for the majority of chicks in many years it would be better if they were born earlier. On the other hand, early in the season temperatures are lower on average, which can be disadvantageous for chicks: in colder conditions they need to be brooded longer and less time remains for feeding. In autumn, selective pressures seem to be working that make the birds, both adults and juveniles, leave as soon as possible.

The different time and energy trade-offs for adults in the nesting and chick-rearing period might balance in different directions for species with different breeding systems. Therefore, a variety of optimality rules with respect to timing of breeding may apply for species differing in breeding strategy.

A variety of breeding systems occur in the Arctic. The fact that so many arctic species incubate the eggs and/or raise chicks alone shows that there is enough leeway to do this. Given the effect of bad weather on body mass dynamics of uniparental, but not on biparental species (chapter 4), combined with the higher occurrence of nest desertions and the better nest insulation in uni- than in biparental species, the energetic margins are apparently smaller for uniparentals. It is therefore possible that uniparental species have certain physiological adaptations that potentially could increase cold tolerance. For instance the degree to which eggs can withstand the cold without damage to the growing embryo may differ between uniparentals, whose eggs are regularly left unattended, and biparentals with continuous incubation. The temperature to which eggs of uniparentals are warmed is relatively high (mean during breeding bouts 39.5°C, own measurements using a metal egg). This is higher than most incubation temperatures that have been recorded in literature (Webb 1987). Unfortunately we do not have measurements of egg temperatures in biparental species in the same area. Perhaps the regular absences in uniparentals are compensated by a higher temperature during brooding bouts?

Figure 10.8. Selective forces on timing of breeding for uniparental and biparental incubators and chicks. Availability of surface-active arthropods (grey line) has an optimum in July. White arrows indicate the different phases within the season. Black arrows indicate the directions of selective pressures acting on adults (both uniparentals and biparentals) and chicks.



The effect of arrival date and arrival condition on reproductive success

The patterns and processes described above affect the optimal timing of breeding in various ways. This information can be used to describe the effect of the timing of and condition at arrival on the reproductive success: a concept that is central in models of migration (Weber et al. 1998; Weber et al. 1999; Klaassen and Ens 2001). This function is referred to as the 'terminal reward' and provides the basis for formulating the optimal behaviour decision for each time/state combination. The aim of this project was to measure reproductive success in shorebirds in relation to arrival date and condition. This would then provide the necessary input for the terminal reward function. Since it turned out to be very difficult to collect this information on the tundra, we applied a more indirect approach where we concentrated on identifying the energetic constraints that shorebirds face during the breeding season. I will not describe here in detail how we eventually derived the terminal function quantitatively based on our field data (Ens et al. 2006), but try to show how the information discussed above was used in a more conceptual way.

Adult survival upon arrival

Upon arrival, shorebirds can use their stores to overcome the first days when the tundra is still snow covered (chapter 2). When snow and ice conditions make feeding impossible for a time that exceeds the capacity of the birds' nutrient stores they face the possibility that they starve. The survival time under starving conditions can be estimated given the bird's fuel stores upon arrival, an estimate of energy expenditure and the probability that starving conditions prevail for this long after each possible arrival date (based on weather data). The resulting probability of survival is largest for birds that arrive with the largest stores and increases with arrival date, due to the fact that the food situation improves and temperatures increase (figure 10.9a). This approach assumes that there is no other source of mortality on the breeding grounds besides starvation risk (which is not entirely realistic given the presence of predators such as peregrines (Schekkerman et al. 2004)).

Length of prelaying period

Upon arrival on the breeding grounds, arctic shorebirds need time to assemble nutrients for transformation of body organs and for egg formation (Morrison et al. 2005). It is likely that arrival mass also influences the interval between arrival and egg-laying. But to date there is no information on the magnitude of this effect. To be able to model all following parameters, this interval needs to be estimated.

Nest survival

The increased risk of nest predation encountered early in the season, due to the fact that predation rates are higher when snow-free patches are scarce, can be modelled as a function of snow cover (figure 10.9b). Predation rates are highly variable between years (indicated by different baseline predation rates) and snow cover has only a limited effect on nest survival. This effect is even partly compensated by the higher probability that early-lost clutches are replaced. The nest survival of replacement clutches is unaffected by snow, as they are laid later in the season.

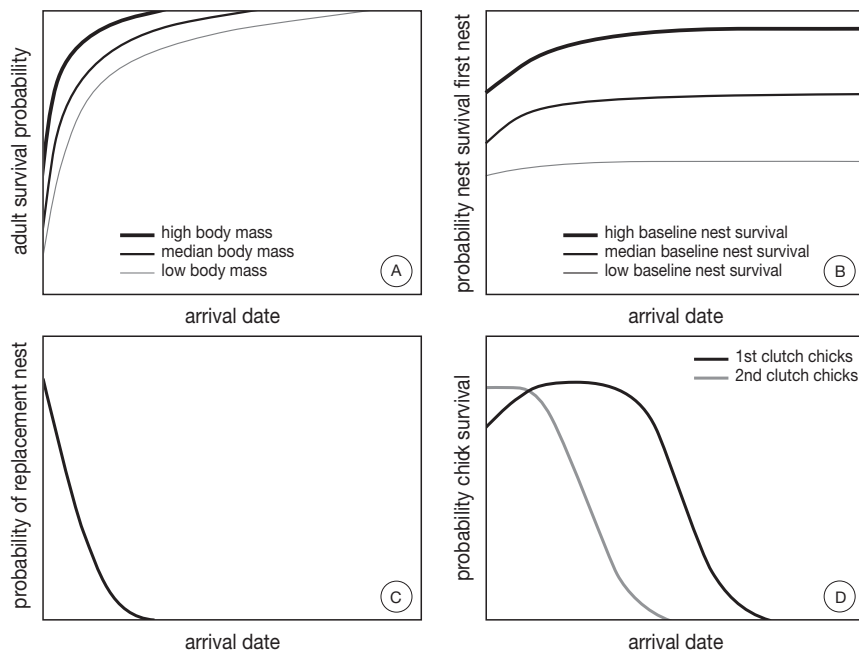
Probability and survival of replacement clutches

When a clutch is lost due to predation, some species will produce a replacement clutch, but only if the season has not progressed too far. The degree to what this will happen depends on the species and the date on which the nest is predated. The production of a new clutch will also take some days. The probability of a replacement being produced decreases rapidly by late June (figure 10.9c). Because of the later starting date the survival of these second clutches is not likely to suffer from the increased predation caused by snow cover, as is the case in the first clutches.

Chick survival

Whether or not chicks manage to fledge successfully depends on the food availability at the time when they hatch and in the period thereafter (chapter 9). Based on assumptions about the necessary food availability for sufficient growth, on how many days of the growth period this level should be reached, and the probability of encountering these levels derived from longterm predictions (chapter 9), the probability for chick survival can be modelled (figure 10.9d). The survival of chicks originating from second clutches can be modelled in the same way, taking into account the later hatching date.

Figure 10.9. Illustrations of the various elements that together were used to construct the terminal reward function.



Reproductive success

The reproductive success can then be estimated combining all these probabilities (figure 10.10). Reproductive success depends on the survival of the adult upon arrival on the breeding grounds and is made up of the sum of the contributions of first clutches and replacement clutches. Success of each of these clutches is the product of hatching success and chick survival. Birds that arrive with large stores should arrive relatively early, while birds arriving with low stores should arrive later to avoid the risk of starvation at this time. The optimal arrival date will thus vary between individuals.

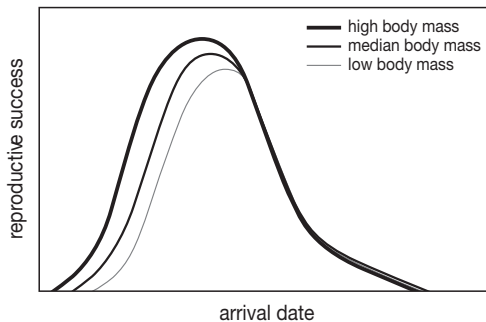


Figure 10.10. Reproductive success as a function of arrival date for a shorebird with three different levels of arrival body mass.

It is obvious that this approach represents a simplification of all potential factors involved. For instance, the effects of adult energetic requirements during breeding, or the predation probability caused by other factors than snow cover, have not been taken into account. The prerequisite for incorporating certain factors in the model is that the relationship with arrival date can be quantified. For some factors this is not yet possible.

Using dunlin as a model species, we quantified the terminal reward function for birds arriving with different body masses (Ens et al. 2006, figure 10.11). Through the effect of adult survival, reproduction in the current year depends not only on arrival date but also on arrival mass. Birds that carry large stores do best by arriving in early June, birds with low stores run a high risk of starvation at this time and would best arrive in mid-June, but they will have a lower reproductive output anyway.

With the terminal reward function quantified, it is interesting to compare it to arrival dates and mass observed. In our study area we only have good data on arrival dates for 2001 and 2002, because in those years we could observe the return of the colourringed individuals (figure 10.11). These observations showed that dunlin arrived in Taimyr in 2001 and 2002 between 6 and 17 June (Schekkerman et al. 2004), which is relatively early compared with predicted arrival dates (figure 10.11). Recorded arrival masses were in the range between 42 and 57 g (mean 48.9 g), levels that are represented by the middle lines in figure 10.11. This discrepancy might be explained by the fact that dunlin is a territorial species and the model did not take into account early arrival associated with competing for the best breeding sites (Kokko 1999). This nicely illustrates that the terminal reward model in its current state is still not finished, but should be developed further on the basis of new empirical information.

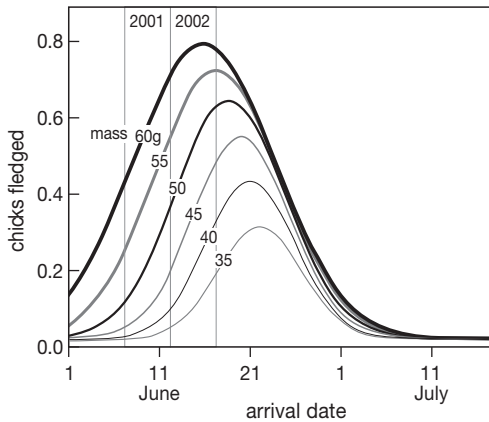


Figure 10.11. Smoothed current reproductive success for Taimyr breeding dunlin as a function of arrival date and arrival mass (in analogy with Ens et al. 2006). The vertical lines indicates arrival period at their breeding area in Taimyr in 2001 and 2002 (Schekkerman et al. 2004).

Arctic shorebirds in a changing world

In a recent review, Meltofte et al. (in press) have summarised the findings from a workshop held in 2004 on the effects of climate change on arctic breeding shorebirds. This multi-authored paper brought together the views of 18 researchers of arctic shorebirds on the effects of environmental forcing on different aspects of the breeding season. Without going in too much detail, the essence of the views on how climatic change might change this, based on current scenarios, is that arctic breeding shorebirds may benefit from it in the short term by an increase in both survival and productivity, although different rates in response to climate change of the timing of food availability and timing of reproduction may deteriorate this prospect. Based on our current knowledge there are no indications that the part of the summer season with high food availability (and therefore of probabilities for reproduction), will be prolonged, even if the onset of the season is advancing. In the long term however, habitat changes both on the breeding grounds and on the temperate and tropical nonbreeding areas may put arctic breeding shorebirds under considerable pressure and may bring some of them near to extinction. Especially the species of the high arctic tundra are at risk; because of the projected northward shifts of habitat zones, this is the first habitat that will be pushed over the edge of the continents.

Given the recent alarming news of the disappearance of the permanent ice on the North Pole, the disappearance of the sea ice (Holland et al. 2006) might accelerate these developments. Currently the climate on the fringes of the arctic land is greatly influenced by that sea ice. An open sea without floating ice will greatly alter the local weather. How this will affect breeding circumstances for shorebirds is not at all predictable but the impact will probably outweigh all other climate driven gradual changes.

Research perspectives

The three years of research at Medusa Bay have yielded 'many new insights' as one of our Russian camp members used to say. Our studies, so far, have been descriptive rather than experimental, a quality of our science that regretfully seems to have lost most of its appreciation, especially with the more competitive scientific journals. However, in the case of a system with many unknowns, even in basic natural history, it is a starting point that cannot be passed by. The knowledge on arctic breeding shorebirds is still miles behind that of well-

studied model species like great tits or pied flycatchers. I hope our studies have contributed to the understanding of the basic mechanisms that set the limits for arctic breeding in shorebirds. There are still many unknowns of course and fields that definitely call for further studies are:

- Mechanisms in the physiology of eggs, chicks and parents that enable breeding in the Arctic.
- Detailed studies on the relation between food abundance and intake rates of parents and chicks. Do intake rates, indeed decrease in bad weather? What is the role of buried larvae, earthworms or even berries for adults? (especially early in the season when arthropod abundance is still low)
- Further development of the migration models to which the 'terminal reward' was contributed by this study to ultimately be able to assess the impact of cumulative effects on shorebird populations.
- Testing whether the patterns found in arthropod abundance and the indications for an advancement of the seasonal peak is a pattern that is more general for arctic tundras.
- The double clutch breeding system of little stints is still poorly understood. Do both nests that a female produce have the same father? Or does the female go to a different area and finds a new mate after she laid the first clutch?
- The coexistence of uni- and biparental systems: given the great advantage of two times four instead of one time four eggs, why does the uniparental strategy not occur in more species? Is the occurrence of uniparentality related to longevity of the species? Could it be that for shortlived species that breed in an area with high predation rates in two out of three years fitness can be optimized by laying more eggs? If breeding success is so dependent on the local prey and predator situation, is it better to spread the predation risk by making two nests?



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Samenvatting



Veel steltlopers zijn lange afstandtrekkers: ze brengen de winter door in gematigde of tropische streken en trekken in het voorjaar noordwaarts om te broeden op het noordelijk halfrond. Tijdens drie zomers (2000-2002) hebben we in arctisch Siberië, op het Taimyr schiereiland (figuur 1.5) onderzocht hoe steltlopers het in de korte arctische zomer, die wordt gekenmerkt door een uiterst grillig klimaat, voor elkaar krijgen om succesvol te broeden. Daarbij lag de focus op het belang van de timing. De timing van aankomst op de toendra heeft gevolgen voor het hele verdere broedseizoen: het tijdstip van de eileg en van het uitkomen van de eieren, voor de kuikengroei en voor het moment van vertrek van de toendra.

Het belang van timing en conditie

We wilden graag weten wat het effect is van de aankomstdatum en -conditie in de toendra op het broedsucces. Is het zo dat vogels die vroeg aankomen succesvoller zijn en meer jongen groot kunnen brengen dan vogels die later aankomen? En is het zo dat vogels die met een goede conditie aankomen ook een betere kans op een goed broedsucces hebben dan vogels met een slechtere conditie? Het verband tussen aankomst en de rest van het broedseizoen vormt een belangrijk onderdeel van een rekenkundig model dat de voorjaarstrek van steltlopers beschrijft. Vanaf hun vertrek van de overwinteringsgebieden in Afrika beschrijft het trekmodel stap voor stap wat er gebeurt. Ze bereiden zich voor op de trek door op te vetten. Dat gebeurt met een bepaalde snelheid en op een gegeven moment hebben ze genoeg energie om de volgende etappe naar de Waddenzee af te leggen. Ook hier vetten ze weer op en vertrekken dan richting Siberië. Zo'n model is niets anders dan een versimpelde weergave van de werkelijkheid, maar omdat de belangrijkste processen erin zijn opgenomen, biedt het de mogelijkheid om een voorspelling over het optimale trekgedrag van steltlopers te maken. Dat model kon ontwikkeld worden omdat verschillende processen van de voorjaarstrek, zoals bijvoorbeeld de energiebehoefte en -beschikbaarheid in een overwinteringsgebied als de Waddenzee, en tijdens de trek al goed bestudeerd

zijn. Wat er eigenlijk nog ontbrak was informatie over het verband tussen de timing van de trek, de conditie bij aankomst in het broedgebied en het daaropvolgende broedsucces, ook wel de 'terminal reward' genoemd. Deze term laat zich lastig vertalen, maar misschien komt 'eindopbrengst' nog wel het dichtst in de buurt (figuur 1.2).

Als dit model eenmaal goed is opgetuigd kun je bijvoorbeeld bekijken wat er gebeurt wanneer het klimaat verandert en daarmee het voedsel, en een vogel die in het voorjaar uit de Waddenzee wil vertrekken niet voldoende heeft kunnen opvetten. Je kunt vervolgens berekenen waar dit dier uiterlijk een tussenstop moet maken, hoeveel hij dan minimaal moeten opvetten om het volgende station te bereiken. En uiteindelijk kun je ook berekenen wat zijn maximale broedsucces zal zijn. Zo dient dit model uiteindelijk ook beschermingsdoeleinden: je kunt aangeven waar de zwakste schakel op een trekroute van een bepaalde soort ligt. En als er één van de gebieden langs de trekroute bedreigd wordt, kun je niet alleen uitrekenen wat daarvan de consequenties zullen zijn, maar kun je ook adviseren over beheer.

De oorspronkelijke bedoeling was dat we steltlopers zouden vangen bij aankomst, en daarna kleurringen zodat ze individueel herkenbaar zouden worden. Deze dieren zouden we dan door het seizoen volgen om te kijken wat er van hun broedinspanningen terecht kwam. Op die manier zouden we de aankomstconditie en -datum kunnen relateren aan het broedsucces. Dat klinkt simpel maar het probleem was dat de vogels die we vingen niet in het gebied bleven, maar doorvlogen naar gebieden verder weg om te gaan broeden. Daarom hebben we uiteindelijk op een alternatieve aanpak ingezet. We hebben geprobeerd in kaart te brengen wat voor de ouders en de kuikens moeilijke perioden zijn; wanneer lopen ze tegen de grenzen aan van wat haalbaar is in zo'n omgeving. Met die informatie kan je vervolgens boven water te krijgen wat de selectiedrukken zijn die de timing van broeden sturen. Welke factoren zorgen ervoor dat de timing naar voren schuift of naar achteren?

Een veelgebruikte eenheid in de ecologie om te meten hoe zwaar dieren het hebben en waar hun beperkingen liggen is energie. Energie wordt opgenomen in de vorm van voedsel. Daarom hebben we het seizoenspatroon van het belangrijkste voedsel, insecten, in kaart gebracht en dit vergeleken met de energetische behoeften en prestaties van ouders en kuikens door het seizoen (energie-uitgave, conditie, groei en beschikbare foerageertijd). Daarmee kun je ook vergelijkingen maken tussen soorten die verschillen in broedstrategie.

Een- en tweeoudergezinnen

Bij steltlopers komen allerhande varianten van broedstrategieën voor. Aan het ene uiterste is de rol van het mannetje beperkt tot het bevruchten van de eieren en komt hij niet eens mee naar de toendra, zoals bij kemphanen, aan het andere uiterste zijn er soorten waarbij de partners de zorg voor eieren en kuikens eerlijk verdelen. Daar tussenin zitten nog allerlei varianten waarbij de ouderlijke zorg meer of minder gelijk verdeeld wordt. Het maakt voor de energiehuishouding nogal wat uit of je als ouder in je eentje voor de eieren en/of kuikens moet zorgen of dat je de ouderlijke zorg kunt delen met je partner. Soorten die de eieren alleen moeten uitbroeden, zoals kleine strandlopers, moeten een zorgvuldige balans zien te vinden tussen tijd die nodig is om de eieren warm te houden en tijd om voedsel te zoeken. Een evenredige verdeling in de broedzorg heeft als voordeel dat beide ouders de helft van de tijd aan iets anders kunnen besteden. De variatie in de verschillende soort broedstrategieën is een heel mooi middel om te onderzoeken waar de energetische grenzen liggen van dieren die zich voortplanten in een relatief onherbergzaam gebied met een grillig klimaat. Zo hebben we ontdekt dat de meeste alleenbroedende soorten later aankomen op de toendra (hoofdstuk 10), dat ze hun nest beter isoleren dan soorten die de broedzorg delen (hoofdstuk 3) en dat voor hen de incubatieperiode stressvoller is dan de kuikenperiode (hoofdstuk 6).

Grote en kleine soorten

Een ander handig handvat voor ons onderzoek is het feit dat in de Arctis vaak meerdere steltlopersoorten in hetzelfde gebied broeden die variëren in grootte. In de kou is groot zijn handig, dat is de stelregel. Als je groot bent, is je lichaamsoppervlak relatief klein, en verlies je weinig warmte. In veel van de onderzoeken die we uitgevoerd hebben, zijn we door middel van vergelijkingen tussen soorten van verschillende grootte, of tussen individuen van verschillende grootte binnen een soort, wijzer geworden over de beperkingen die broeden in de Arctis met zich meebrengt (hoofdstukken 2, 3, 4). We hebben ontdekt dat kleine strandlopers die noordelijker broeden groter, maar ook zwaarder zijn (hoofdstuk 5), dat kleine soorten meer werk maken van hun nestisolatie dan grotere soorten (hoofdstuk 3) en dat kleinere soorten tijdens de broedtijd extra reserves bij zich hebben om wat beter in te kunnen spelen op slecht weer (hoofdstuk 4).

De timing in de drie seizoenen

Tijdens de drie veldseizoenen hebben we gemeten wanneer de verschillende soorten aankomen op de toendra, wanneer ze beginnen met broeden en wanneer de eieren uitkomen. Bij aankomst begin juni is in de meeste jaren het grootste deel van de toendra nog bedekt met sneeuw. Maar hoeveel sneeuw er nog ligt en het tempo waarmee het verdwijnt varieert sterk van jaar tot jaar. Zelfs binnen de drie jaar van deze studie was dat zo. In 2000 was op 5 juni al de helft van het studiegebied sneeuwvrij, terwijl op dezelfde datum in 2001 de sneeuwbedekking nog 80% bedroeg en in 2002 zelfs bijna 100% (figuur 10.1).

Omdat het verschijnen van de insecten sterk samenhangt met weersomstandigheden, laat het verloop van het insectenaanbod en de piek daarin ook sterke variatie tussen jaren zien (figuur 10.1). Ondanks deze variatie was de timing van broeden vergelijkbaar in 2000 en 2001. Maar in 2002, het laatste jaar qua sneeuwsmeelt, waren de mediane legdata van de verschillende soorten 4-10 en 2-9 dagen later dan in 2000 en 2001. Daarbij was het seizoen veel meer gecomprimeerd. In 2002 werden alle nesten binnen een periode van twee weken gelegd, terwijl dit in een vroeger jaar gemakkelijk vier weken bedraagt.

Als gevolg van de late insectenpiek in 2001 en 2002, werden de meeste kuikens pas geboren op het moment dat het voedselaanbod zijn piek had bereikt (figuur 10.1). In 2002 groeiden de kuikens op in de periode waarin het voedsel al weer afnam. In 2001 namen de aantallen insecten zelfs alweer af voordat de eerste kuikens geboren werden. In die jaren werden de kuikens dus relatief laat geboren.



Factoren die invloed hebben op de timing

Alle artikelen uit dit proefschrift behandelen factoren die op de een of andere manier invloed hebben op de timing van broeden. Al deze factoren, zoals bijvoorbeeld de hoeveelheid sneeuw bij aankomst in het voorjaar, de beschikbaarheid van het voedsel, de energiebehoefte, predatie door vossen en andere rovers, sturen op de een of andere manier het moment van broeden en dus ook het moment van het uitkomen van de eieren. Deze factoren werken voor soorten die alleen broeden anders door dan voor soorten die samen broeden. Voor de alleenbroeders is het zaak dat er in de broedperiode voldoende voedsel beschikbaar is, zodat ze in de spaarzame momenten dat ze even van het nest kunnen ook snel genoeg voedsel binnen kunnen krijgen om de drie weken tot het uitkomen van de eieren uit te kunnen zitten. De soorten die de broedzorg delen zitten ruimer in hun tijd. Je ziet dan ook dat de soorten die alleen broeden, later in het seizoen aankomen (figuur 10.2) en over het algemeen later beginnen met broeden. Er is dan meer voedsel en het is warmer.

Daarbij komt ook nog dat de belangen van kuikens wel eens anders kunnen liggen dan die voor de ouders. Het voedselaanbod is sterk gepiekt (hoofdstuk 9) en in de meeste jaren worden de kuikens pas geboren als het voedselaanbod alweer aan het dalen is. Dat is ongunstig voor de kuikens, maar de ouders moeten natuurlijk ook voldoende voedsel kunnen vinden. Dus vanuit het belang van de kuikens zouden de ouders eerder moeten beginnen met broeden, maar vanuit het belang van de ouders is dat misschien helemaal niet haalbaar. Vroeg in het voorjaar is er nog weinig voedsel.

Nesten worden op de grond gelegd en kunnen pas gemaakt worden als er een plek is om dat te doen. Er moeten dus eerst sneeuwvrije plekken zijn. Maar nesten die gelegd zijn op de eerste sneeuwvrije plekken gelegd lopen een grotere kans gepredeerd te worden. Rovers zoals poolvossen zoeken het gebied systematisch af en hoe minder gebied er sneeuwvrij is hoe groter de kans dat ze een nest tegenkomen. De sneeuw en de snelheid van smelten werkt ook nog op een andere manier door in de kans dat de eieren opgegeten worden. Lemmingen die in de winter in uitgebreide gangenstelsels onder de sneeuw leven hebben het in het voorjaar even een periode behoorlijk lastig. Hun winterverblijf verdwijnt met de sneeuw en hun zomerverblijven, uitgebreide gangenstelsels in de toendra zijn nog bevroren en niet toegankelijk. Ze kunnen dan eigenlijk geen kant uit en vormen een makkelijke prooi voor predatoren. Op die manier leiden ze de aandacht af van steltlopernesten. De kans op predatie vertoont dus in sommige jaren een seizoenspatroon (figuur 10.4) en in dat soort jaren is het gunstig om vroeg te broeden. In echte lemming-

piekjaren, zijn er het hele seizoen voldoende lemmingen en vormt predatie minder een probleem. In lemmingarme jaren en in jaren waarin de sneeuw snel smelt, zal dit mechanisme niet optreden. De effecten die veroorzaakt worden door sneeuwbedekking hangen dus samen met de lemmingsituatie en de reactie van predatoren.

Als het eerste legsel is gepredeerd leggen sommige steltlopersoorten een nieuw legsel ter vervanging. Maar in de praktijk gebeurt dat alleen in vroege jaren en bij vroege legfels. In 2000 werden veel van de bonte strandlopernesten opgeruimd door poolvossen, maar alleen de ouders van de nesten die voor 25 juni werden gepredeerd legden opnieuw (figuur 10.5). Nesten die pas na die datum gepredeerd werden, werden niet meer vervangen. In de andere twee jaren werden verdwenen nesten nauwelijks vervangen. Alleen ouders die hun eerste nest vroeg leggen hebben dus zo'n herkansing.

Eerder beginnen met broeden houdt ook in dat de vogels eerder in het broedgebied aan moeten komen en dus ofwel eerder uit het overwinteringsgebied moeten vertrekken of de reis moeten verkorten. Vroeger aankomen is een riskante onderneming, want de kans dat de toendra bij aankomst nog bedekt is onder een pak sneeuw is niet onaanzienlijk. Zeker voor langeafstandtrekkers is het ondoenlijk om vanuit de overwinteringsgebieden, duizenden kilometers ver weg in te schatten of het een vroeg of een laat voorjaar zal worden. Om dit risico te verkleinen leggen steltlopers het laatste stuk naar hun broedgebied waarschijnlijk niet in een keer af, maar benaderen ze hun broedplek voorzichtiger, waarbij ze telkens tussenstops maken. Dat blijkt wel uit waarnemingen van gekleurringde bonte strandlopers in ons gebied: in het begin van het seizoen zagen we nog nauwelijks lokale (=geringd in het gebied in het voorgaande jaar) broedvogels tussen de bonte strandlopers, maar in de loop van het voorjaar werd het aandeel gekleurringde vogels steeds groter (figuur 10.3). De veiligste strategie is dan elk jaar op dezelfde datum aan te komen met wat reserves om de eerste dagen door te komen en stapsgewijs het uiteindelijke broedgebied te benaderen (hoofdstuk 2).

Vroeg in het seizoen is de permafrost nog erg ondiep, en het warmhouden van de eieren, die praktisch direct op deze ijslaag liggen kost dan meer energie dan later in het seizoen, wanneer de permafrostlaag dieper in de grond zit (hoofdstuk 3). Uit de metingen aan nestisolatie van de verschillende soorten bleken vooral de kleine soorten, die toevallig ook de soorten zijn die alleen broeden, het meeste werk te maken van de nestisolatie. Met name voor deze soorten is een vroege start misschien energetisch niet haalbaar omdat het warmhouden van de eieren dan teveel energie kost.

Voedsel is dus belangrijk voor de timing omdat het een seizoensverloop vertoont, maar ook de energiebehoefte varieert met het seizoen. Niet alleen veranderen de activiteiten van de ouders, ook de energie die nodig is om op temperatuur te blijven verandert. Aan het begin van het seizoen zijn temperaturen onder 0°C heel gewoon, maar in de loop van de zomer wordt het warmer. Voor kuikens werkt dit nog eens extra door, omdat ze in hun eerste levensweek hun eigen lichaamstemperatuur niet op peil kunnen houden. Daarom worden ze bebroed door hun ouders, maar de tijd die dat kost gaat af van de foerageertijd. Als ze net de pech hebben geboren te worden in een periode met regen of sneeuw kan dat fataal zijn. Voor de energie-uitgave van de kuikens is het het beste als ze geboren worden wanneer de kans op goed weer het grootste is, midden in de zomer dus.

Aan het eind van de zomer, in augustus, wordt het tijd om de toendra te gaan verlaten. Vanaf september valt alweer de eerste permanente sneeuw en is er weinig voedsel meer te vinden. Er zijn aanwijzingen dat de vogels nogal haast hebben om weg te komen. De bonte strandloper is een van de weinige soorten die beginnen met het ruien van de vleugelveren tijdens het broeden. Aan het eind van het broedseizoen zijn ze daar nog niet helemaal mee klaar. De vogels die bezig waren met de zuidwaartse trek die wij vingen in de nazomer vertoonden nog bijna allemaal actieve vleugelruï (figuur 10.6). Vliegen met vleugels waarvan sommige veren nog niet volledig uitgegroeid zijn kost meer energie dan met volledige volgroeide veren. Daarom is het vreemd dat ze toch al vertrekken en niet wachten tot ze klaar zijn met de rui. Kennelijk is het belangrijk om zo vroeg mogelijk de toendra te verlaten. Van krombekken weten we dat de eerste vogels alweer half juli door de Waddenzee trekken. Dat zijn de mannetjes, die de toendra verlaten hebben nadat de eieren gelegd zijn. Maar ook van kanoeten weten we dat ze zo snel als mogelijk vertrekken.



En er zijn bovendien weinig aanwijzingen dat steltlopers echt opvetten, zoals ze doen als ze in het voorjaar naar de toendra gaan (figuur 10.7). Ook de vliegvlugge kuikens vetten aan het eind van de zomer niet op voordat ze aan de reis beginnen. Waarschijnlijk is het dus gunstig om vroeg te vertrekken; dat kan ermee te maken hebben dat het voedsel op de toendra begint op te raken maar ook met de situatie in de gebieden die ze op de terugweg aandoen. Zo kan het zijn dat er daar een sterke competitie om voedsel is, of voor goede, veilige gebieden om te ruïen (=beschut tegen mogelijke predatoren). Het zou ook kunnen dat ze, door vroeg te vertrekken, de golf aan roofvogels voorblijven die ook weer zuidwaarts zullen gaan.

Er zijn dus nogal wat krachten in het spel die de optimale broeddatum beïnvloeden (figuur 10.8). Er zijn factoren waarvan je verwacht dat ze leiden tot een vervroeging van de datum, maar ook factoren die zorgen dat de datum naar achteren schuift. Voor soorten die alleen broeden pakt dat anders uit dan voor soorten die de broedzorg delen en voor kuikens ziet de optimale timing er nog anders uit.

Het effect van timing en conditie op het broedsucces

De ingrediënten die we in de verschillende deelonderzoeken bijeen hebben gesprokeld hebben we gebruikt om het verband tussen aankomstconditie en -datum op het broedsucces te bepalen. De kans dat een steltloper succesvol broedt hangt af van meerdere factoren (figuur 10.9). Aan de hand van gegevens over de bonte strandloper hebben we de 'terminal reward' functie bepaald (zie introductie). Hierbij hebben we berekend wat de beste aankomstdatum zou zijn voor dieren met verschillend lichaamsgewicht (figuur 10.11). Daaruit blijkt dat vogels die met een grote reserves aankomen het zich kunnen permitteren om vroeg (tweede week van juni) te arriveren. Vogels zonder reserves moeten later aankomen om het risico op een sneeuwbedekte toendra en verhongering te vermijden. Deze dieren zullen sowieso een lager broedsucces hebben. Vergeleken met de modelvoorspellingen zijn de werkelijke aankomstdata aan de vroege kant. Uit waarnemingen uit het veld weten we dat bonte strandlopers in Taimyr arriveerden tussen 6 and 17 juni in 2001 en 2002 (figuur 10.11). Dat verschil wordt waarschijnlijk veroorzaakt doordat het model geen rekening houdt met het feit dat bonte strandlopers waarschijnlijk ook tijd nodig hebben om een territorium te bemachtigen. Dat illustreert gelijk de beperkingen van het model en de noodzaak het verder uit te bouwen. Zo zijn bijvoorbeeld ook factoren als de energiebehoefte van volwassen vogels tijdens het broeden en de kans op predatie die veroorzaakt worden door andere factoren dan de sneeuwbedekking niet meegenomen. De reden daarvan is simpel: ze zijn (nog) niet (voldoende) gekwantificeerd.

De Arctis in een veranderende wereld

Het is niet eenvoudig om te voorspellen wat er met steltlopers in de Arctis gaat gebeuren als gevolg van de klimaatveranderingen. De voorspelling is dat de Arctis meer dan andere gebieden de gevolgen zal gaan ondervinden van de opwarming van de aarde. Niet alleen zal de temperatuur toenemen, maar ook de hoeveelheid neerslag, terwijl de periode dat er sneeuw ligt zal afnemen. Als gevolg daarvan zullen er verschuivingen optreden in vegetatiezones. In een recent artikel hebben verschillende arctische steltloperonderzoekers zich over de vraag gebogen wat voor effect deze ontwikkelingen voor steltlopers zullen hebben. Over veranderingen op korte termijn die vooral een graduele verandering betreffen valt nog wel iets zinnigs te zeggen. Verdere opwarming zou kunnen resulteren in een betere overleving van de ouders, een beter broedsucces en dus meer kuikens. Bij hogere temperaturen groeien kuikens immers beter en is het leven voor de ouders ook eenvoudiger. Het kan echter ook anders uitpakken. Uit onze analyses bleek dat het door de sterke jaar op jaarvariatie moeilijk is om te voorspellen wanneer de piek in het voedselaanbod zal vallen, maar dat de kans om die piek te treffen het grootst is als steltlopers zo vroeg mogelijk beginnen met broeden, dat wil zeggen zo gauw de sneeuw begint te smelten. Verdere vervroeging in de datum van sneeuwsmeelt kan ertoe leiden dat steltlopers, als ze niet eerder aankomen op de toendra dan ze nu doen, de piek gaan missen en hun kuikens niet snel genoeg kunnen groeien. Ook de voorspelling dat de neerslag in de zomer gaat toenemen is niet gunstig voor kuikens. Insecten zijn dan moeilijker te vinden.

Op langere termijn, waarin het waarschijnlijk is dat er veranderingen in het ecosysteem drastischer zullen zijn, is het veel moeilijker te voorspellen wat er gaat gebeuren. De verspreiding van de meeste arctische broedende steltlopers is beperkt tot een bepaalde toendrazone variërend van de relatief weelderige sub-arctische en laag-arctische toendra tot de drogere en schralere hoog-arctische toendra. Elke soort is dus afhankelijk van waar een bepaald toendratype voorkomt en over welke oppervlakte. Behalve wanneer soorten zich aanpassen en uitwijken naar andere vegetatiezones, valt het dus te verwachten dat veranderingen in vegetatiezones als gevolg van klimaatverandering invloed zullen hebben op het broedareaal. De verwachting is dat de sub-arctische zone met hogere vegetatie en de gematigde bossen zullen opschuiven naar het noorden. Dit zal het broedareaal van arctische steltlopersoorten verkleinen. Volgens huidige klimaatscenario's zal ongeveer de helft van de Arctis nog binnen deze eeuw veranderen naar sub-arctische struikzone, waarna het op langere termijn uiteindelijk in bos verandert. Deze ontwikkelingen pakken het meest dramatisch uit voor soorten die nu broeden in de hoog-arctische zone,

zoals kanoet en drieteenstrandloper. Die zone raakt steeds meer bekend tussen de oprukkende sub-arctische struikzone en de Arctische Oceaan en zal uiteindelijk als eerste over de rand van het continent schuiven. Wanneer het zee-ijs gaat verdwijnen, wat volgens de meest recent berichten veel sneller is aan het gebeuren dan tot nu toe voorspeld, zal de invloed van de zee op het land veranderen. Een open zee zonder drijvend ijs in de zomer zal het lokale weer sterk beïnvloeden. Hoe dit de omstandigheden voor steltlopers gaat veranderen is koffiedikkijkerij, maar het effect zal waarschijnlijk alle andere geleidelijke klimaateffecten overtreffen.

Nieuwe vragen

Na drie jaar onderzoek zijn we een hoop meer te weten gekomen over de energetische grenzen waar steltlopers mee te maken krijgen in de arctische toendra van Siberië. Maar zoals bij elk onderzoek roept elke nieuwe ontdekking weer nieuwe vragen op.

Over het naast elkaar voorkomen van verschillende broedsystemen bijvoorbeeld. Waarom komt de dubbellegsel strategie van de kleine strandloper niet bij meer soorten voor? Het grote voordeel van twee nesten is natuurlijk dat de dieren de ouder zijn van twee keer vier in plaats van één keer vier eieren. In het ideale geval kan dat twee keer zoveel kuikens opleveren. Is het misschien zo dat het voorkomen van dit systeem vooral gerelateerd is aan de levensduur van een soort? Is het voor kortlevende soorten, die in een gebied broeden waar de kans op predatie in twee van de drie jaar erg groot is, gunstig om te investeren in veel eieren verdeeld over twee legfels om zodoende de kans op predatie te verkleinen? Als het broedsucces zo sterk afhangt van het voorkomen van predatoren is het misschien goed om aan risicospreiding te doen. En hoe kan het dat eieren van alleenbroedende soorten zo vaak



onbebroed achterblijven en er toch even lang over doen om uit te komen? Hebben eieren en of kuikens fysiologische aanpassingen die dit mogelijk maken? Iets anders waar we nog niet aan toe gekomen zijn is om te onderzoeken is hoe de voedselopname afhangt van het weer. We hebben gezien dat de groeisnelheid afneemt bij slecht weer en dat dat met temperatuur en voedsel te maken heeft. Maar komt dat omdat er wel insecten zijn, maar deze niet actief zijn en de kuikens ze niet kunnen vinden? En wat is de rol van bessen, ingegraven larven en wormen? Met name vroeg in het seizoen, als er nog weinig insecten zijn, zou dat een alternatieve voedselbron voor de volwassen vogels kunnen zijn. Ook zijn we nog niet klaar met het trekmodel waar de 'terminal reward' model deel van uitmaakt. Verdere ontwikkeling daarvan maakt het op termijn mogelijk om in te kunnen schatten wat het effect zal zijn van ontwikkelingen die zich gelijktijdig voordoen. Onze constatering dat de timing van de voedselpiek vroeger lijkt te worden geldt natuurlijk alleen voor ons kleine studiegebied. Het zou goed zijn om te testen of dit een meer universeel patroon is dat ook in andere arctische gebieden te zien is.

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Tot slot

Op het moment dat ik dit schrijf zit ik op een vliegbasis ergens in het oosten van Groenland. Afgezien van de landingsbaan en een paar gebouwen is hier helemaal niets. Ik ben de enige hier van ons team, dat deze zomer onderzoek doet aan drieteenstrandlopers in Zackenberg, een Deens onderzoeksstation. De anderen, Jeroen Reneerkens, Joop Jukema, Koos Dijksterhuis en Hans Schekkerman, zijn al in Zackenberg, zo'n 500 km verder naar het noorden. Er gaat maar één keer per week een vliegtuig heen en daar moet ik nu nog drie dagen op wachten. Er is misschien geen betere plek, teruggeworpen op mezelf en omringd door de toendra, om het dankwoord voor mijn proefschrift te schrijven.

Toen ik in 1986 met mijn studie biologie aan de Universiteit van Utrecht begon had ik nog geen flauw idee welke richting ik op wilde. Mijn verwachting dat de studie in ieder geval veel veldwerk zou omvatten, bleek bepaald niet te kloppen: in het hele eerste jaar heb ik welgeteld één dag veldwerk gedaan, dat bestond uit het stofzuigen van struiken om insecten te bemonsteren. Met een sterke nadruk op moleculaire, biomedische en genetische werkelden was Utrecht duidelijk niet de plek voor mij. Inmiddels was ik er wel achter dat ik met organismen wilde werken die ik kon zien en aanraken. In de tweede helft van mijn studie ging ik dus op zoek naar een plek die beter paste en vond die in het Nederlands Instituut voor Onderzoek der Zee (NIOZ) op Texel. Daar in de, toen beginnende, groep van Theunis Piersma voelde ik me meteen op mijn plek. Samen met Yvonne Verkuil deed ik een doctoraal-onderwerp aan de voedselécologie van kanoeten in de Waddenzee. Tegelijkertijd introduceerde Theunis ons in de Groningse school van de dierecologie, iets wat voor zowel Yvonne als mij de basis werd van ons verdere werk. In de jaren daarna genoot ik van de inspirerende omgeving op het NIOZ, de universiteit van Groningen en later ook aan de universiteit van Lund in Zweden. Ik kwam er achter dat een van de grote voordelen van het werken aan trekvogels is dat je met ze mee mag reizen naar exotische oorden zoals Australië en Siberië.

Tegen de tijd dat ik afstudeerde lagen de AIO-banen niet voor het oprapen. Omdat ik niet veel trek had eindeloos te blijven rondhangen als vrijwilliger, iets wat ik die tijd vrij normaal was voor werkeloze biologen, en ik het gevoel had niet langer in de Texelgroep te passen, besloot ik elders een baan te zoeken. Gedurende een aantal jaren werkte ik bij verschillende organisaties zoals SOVON, Vogelbescherming Nederland en Bureau Waardenburg in toegepast onderzoek. Ik had er aardige collega's en van tijd tot tijd leuke projecten, maar het idee van een eigen onderzoek bleef trekken. Ondertussen probeerde ik mijn werk te combineren met vogelonderzoek op vrijwillige basis. In 1996 bracht ik samen met Leo Bruinzeel, Joop Jukema en Olga Stepanova, mijn eerste bezoek aan Medusa Bay op het Taimyr-schiereiland in Siberië. Diverse pogingen om geld te vinden voor eigen onderzoek in het buitenland waren niet succesvol. Enkele andere opties in Nederland mislukten daarna ook om uiteenlopende redenen. Dus na een poos realiseerde ik me dat het leven niet altijd brengt wat je er van verwacht en ging ik verder op de ingeslagen route: gewoon leuk veldonderzoek doen in mijn vrije tijd en dit combineren met een 'echte' baan in de toegepaste wetenschap.

Door de inspanningen van Jan Veen van Alterra en Gerard Boere van het ministerie van (toen nog) Landbouw, Natuurbeheer en Visserij, was er geld beschikbaar om onderzoek te doen aan steltlopers in Siberië. De Nederlandse overheid had geïnvesteerd in een onderzoeksstation in Medusa Bay en nu was het tijd dat het ook daadwerkelijk gebruikt ging worden. In eerste instantie was er echter slechts geld voor één persoon voor één seizoen en het was onduidelijk of er de volgende jaren ook geld zou zijn. Samen met mijn partner, Hans Schekkerman,

die ook erg gecharmeerd was geraakt van de arctische wereld, besloten we dit project op te pakken. Gedeeltelijk vrijwillig en gedeeltelijk betaald begonnen we aan een expeditie. We genoten erg en voelden ons bevoorrecht om ruim twee maanden in de toendra te mogen doorbrengen. Dat jaar werden we vergezeld door Raymond Klaassen. Het veldseizoen was niet alleen qua onderzoek een succes, het was ook erg gezellig, mede door Raymonds aanstekelijke enthousiasme en onuitputtelijke energie. Nog niet erg bekend met de Russische keuken hadden we de voedselvoorziening volledig aan onze Russische expeditiegenoten overgelaten. Dat was een misrekening die we de daaropvolgende jaren niet meer maakten. Elke dag was er wel weer iets anders op: als eerste verdween de wodka, de jam was na de tweede week al op, de chocolade na de derde, aan groente werd al helemaal niet gedaan en aan het eind van de eerste maand was er ook geen toiletpapier meer. De rest van het seizoen aten we vis met puree. De twee volgende jaren gingen we op dezelfde financiële basis naar Medusa Bay. Hoofdschuddend bekeken de Russen hoe wij, door ervaring wijs geworden, weekpakketten maakten zodat alle lekkere dingen beter gerantsoeneerd waren.

In de drie jaren werden we vergezeld door onze Russische teamgenoten die ieder hun eigen deel van de artische flora en fauna onderzochten: Sergei Karitonov meeuwen, ganzen en roofvogels, Mikhael Berezin insecten, Andrei Bublichenko zoogdieren, Yulia Bublichenko zangvogels, Sofia Rosenfeld, Sergei Khomenko en Tanya Kirikova steltlopers, en Tanya Varlygina en Tanya Pereladova (de Botanyas) de vegetatie. Een aantal van hen was erg bedreven in het ten gehore brengen van, vaak zwaarmoedige, Russische liederen. In 2001 gingen Oscar Langevoord en Leon Peters mee als deelnemers vanuit de WIWO (Werkgroep Internationaal Wad- en Watervogelonderzoek). In 2002 nam Joep de Leeuw deel als vrijwilliger. In datzelfde jaar sloot Kathy Tjørve van de Universiteit van Kaapstad zich ons bij zich aan, om een deel van haar PhD studie aan energetica van groei bij steltloperkuikens te doen. Bij werk in afgelegen gebieden is het gezelschap erg belangrijk en het was erg leuk om elk jaar de verwondering en het enthousiasme te zien van mensen voor wie het allemaal nieuw was. Daardoor realiseerden wij ons zelf ook steeds opnieuw hoe bijzonder het is om in dit soort streken te kunnen werken. Bij de voorbereidingen en de organisatie van de expedities hebben veel personen een belangrijke rol gespeeld. Sergei Kharitonov verzorgde alle administratieve procedures en de reizen in Rusland, de familie Dudko en Alexander Beliaшов in Dikson zorgden voor vervoer naar en van het station en losten kleine en grote



lokale problemen op, Valery Chuprov, de directeur van het Great Arctic Reserve en zijn staf in Dudinka verzorgden de benodigde vergunningen, en Gerard Müskens bracht ons met al onze bagage naar en van Schiphol. Aanvullende financiering voor materiaal- en reiskosten kregen we van NWO (2000), de Animal Behaviour Society (2000) en de European Science Foundation (2001).

Na de drie veldseizoenen begon het duidelijk te worden dat er genoeg materiaal was voor een proefschrift. De gegevens die wij verzameld hadden zouden een deel van de onderbouwing vormen voor een model over vogeltrek, waaraan Bruno Ens, Silke Bauer en Marcel Klaassen samenwerkten. Binnen dit project kreeg ik tijd toebedeeld voor het doen van basale analyses en rapportages. Dat gaf me een begin voor het uiteindelijke schrijfwerk, wat verder vooral in mijn vrije tijd gedaan moest worden.

Door de jaren heen hebben mijn 'bazen' bij Bureau Waardenburg, Sjoerd Dirksen, Martien Meijer en Hans Waardenburg, het mogelijk gemaakt om de hele zomer vrij te nemen. Na het laatste veldseizoen in 2002 ben ik bij het toenmalige RIVO (inmiddels IMARES) gaan werken. Een belangrijke reden daarvoor was dat Hans en ik, naast ons gezamenlijke arctische werk, steeds meer als collega's in samenwerkingsprojecten terecht kwamen. Vandaar de vrij drastische overstap van vogels naar vis. Hoewel ik me in de 'viswereld' nog regelmatig een vreemde eend in de bijt voel, waren de meeste van mijn collega's wel geïnteresseerd in mijn vogelwerk. Vooral Joep de Leeuw, Erwin Winter en Adriaan Rijnsdorp waren altijd bereid mee te denken over een figuur of een artikel. In de laatste fase van schrijven werd mijn zelfopgelegde strakke schema enigszins verlicht door het feit dat het management van IMARES me een aantal weken schrijftijd toebedeelde.

Joop Jukema en Raymond Klaassen zullen mij bijstaan als paranimfen tijdens de ceremonie. Met Joop samen heb ik in 1994 mijn eerst stappen op de toendra gezet bij Kaap Sterlegov. Ik verheug me er op nu na meer dan tien jaar weer samen met hem veldwerk in Groenland te mogen doen! Raymond zette zijn eerst stappen op de toendra in 2000 samen met Hans en mij. Joop en Raymond delen dezelfde passie en enthousiasme voor onderzoek, de toendra en zijn bewoners.



De meeste mensen beschrijven in hun dankwoord hoe stimulerend hun schrijfperiode geweest is door alle discussies met collega's. Mijn ervaring is dat het mijn meest eenzame oefening tot dusver is geweest, schrijvend in mijn kamertje thuis terwijl de meeste van mijn collega's druk bezig waren uit te rekenen hoeveel (of liever gezegd hoe weinig) vis er nog in zee rondzwemt. Dit was natuurlijk het resultaat van mijn nogal ongebruikelijke promotietraject, waarin ik probeerde het fundamentele werk aan steltlopers te combineren met een baan aan toegepaste vragen in de mariene wereld. Het voordeel van die combinatie is dat je gewend bent aan deadlines en efficiënt met je tijd leert omspringen. Het nadeel was dat ik niet rustig de tijd had om allerlei zijpaden te onderzoeken, maar doelgericht moest werken als ik dit binnen afzienbare tijd tot een goed einde wilde brengen.

In de laatste fase hebben Theunis Piersma, Henk Visser, Bruno Ens en natuurlijk Hans veel moeite gestoken in het lezen en becommentariëren van manuscripten, vaak op korte termijn. De laatste week voordat ik het in moest leveren, was het zelfs handig dat Bruno en Hans op een conferentie in Nieuw-Zeeland waren, zodat zij 's nachts konden becommentariëren wat ik overdag geschreven had. Henk Visser geloofde vanaf het begin in dit project en omdat wij slechts een bescheiden onderzoeksbudget hadden, verzorgde hij kosteloos zwaar water en analyses. Door de jaren heen heeft Henk zich altijd bekommerd om de voortgang van het project en ik vind het dan ook heel erg jammer dat hij de afronding niet meer heeft kunnen meemaken.

Het commentaar van Theunis leverde het meeste werk op voor mij, omdat het meestal de structuur van het verhaal betrof. En zelfs als het er nog niet helemaal of helemaal niet was, leek hij wel aan te voelen dat er toch iets goeds aan zat te komen. Dit wordt wel het beste geïllustreerd door zijn woorden in de kantlijn: "ik kan je hier helemaal niet volgen, maar het is vast machtig interessant!". Toen het idee rijpte om een proefschrift te schrijven over het arctische werk was ik blij dat hij mij daarin wilde begeleiden. Ik vind het erg leuk dat hij nu mijn promotor is, zeventien jaar nadat ik als student bij hem begon. Ondanks dat ons contact lange tijd op een laag pitje stond, heb ik altijd de overtuiging gehad dat ik als bioloog gevormd ben door zijn manier van kijken en onderzoeken.



Furthermore I would like to thank Will Cresswell, Joost Tinbergen and Marcel Visser who were willing to be part of the reading committee. Pavel Tomkovich, Hans Meltote and Les Underhill were always willing to share their ideas and knowledge on arctic shorebirds whenever I needed it.

Maria van Leeuwe, Marian Verhage, Marijke Schekkerman en Joep de Leeuw lazen en commentarieerden de Nederlandse teksten met een 'lekenbril'. Louisa Mendes en Anneke Bol (NIOZ) verzorgden de DNA sexe-analyses en Berthe Verstappen van het Centrum voor Isotopen Onderzoek verzorgde de zwaar water analyses.

Ik ben erg blij dat Nicolet Pennekamp de opmaak van mijn proefschrift op zich neemt. Ik heb er alle vertrouwen in dat het resultaat prachtig wordt en dat het niet op een proefschrift lijkt. Dick Visser heeft met zorg de figuren omgetoverd in ware kunstwerkjes. Jan van de Kam heeft tussen twee expedities door tijd gevonden om een mooie selectie van zijn stelfoto's te maken en ik vind het een eer dat zijn foto's in mijn proefschrift staan.

Verder wil ik al mijn familie en vrienden bedanken die altijd interesse toonden en er geloof in hadden dat ik dit werk zou afronden en die bovendien voor de nodige afleiding zorgden. Vanzelfsprekend wil ik mijn ouders en ook tante Wil heel erg bedanken. Ook al was het voor jullie niet altijd even duidelijk wat ik allemaal uitspookte en waarom ik zo nodig telkens naar zulke afgelegen oorden moest, jullie hadden alle begrip, geduld en interesse. Bovendien genoten jullie van de verhalen en plaatjes als we weer terug waren. Ik beseft dat ik erg bevoorrecht ben dit soort ervaringen mee te kunnen maken, iets wat voor jullie generatie helemaal niet was weggelegd.

Dan kom ik toe aan de persoon die het belangrijkste geweest is bij de totstandkoming van dit proefschrift. Niet alleen in het veld, met zijn kennis en ervaring in het vangen en hanteren van vogels, maar ook tijdens de data-analyse en het schrijven was Hans onmisbaar. Ik heb ongelooflijk veel van hem geleerd tijdens de jaren dat we samenwerkten. Samen veldwerk doen als partners mag dan romantisch lijken, het is zeker niet altijd gemakkelijk geweest. Vooral in het organiseren van praktische zaken werden de verschillen in onze karakters ineens erg duidelijk. Verder heeft het ook nadelen om samen met iemand te werken die alom gezien wordt als een gedegen en slimme onderzoeker. Ik heb meermaals mijn eigen inbreng in dit onderzoek naar de buitenwereld moeten verdedigen, hoe oneerlijk dat vaak ook voelde. Natuurlijk is het een resultaat van ons samen, maar dit proefschrift had er niet gelegen zonder de inbreng van elk van ons. Wanneer er in de schrijffase voor de zoveelste keer een manuscript overhoop moest en anders moest opgeschreven, heb ik vaak op het punt gestaan de hele boel in de dichtstbijzijnde hoek te keilen en ermee op te houden. Maar in dit soort situaties hield Hans altijd het hoofd koel en wist me er van te overtuigen dat ik er niet mee op moest houden en dat het de moeite waard was. En dat was het!

