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Behavioural and physiological adaptations of precocial chicks to arctic environments

Karen Krijgsveld

The work presented in this thesis was conducted at the Behavioural Biology Group at the University of Groningen, Netherlands. All studies were approved by the Ethical Committee of the University of Groningen, by the Institutional Animal Care and Use Committee of the University of Missouri–St. Louis and/or by the Canadian Wildlife Service. The research was supported by National Science Foundation (NSF) grant OPP-9423522 awarded to RE Ricklefs and GH Visser. Additional support was received from the Netherlands Organization for Scientific Research (NWO).

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Prof. dr. B.I. Tieleman

The woods are lovely, dark and deep
but I have promises to keep
and miles to go before I sleep
and miles to go before I sleep

Robert Frost

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Chapter 1

Introduction, summary & synthesis

Karen L Krijgsveld

Thesis theme

Growth of an individual encompasses a myriad of physiological and behavioural changes. The most obvious of these is the increase in size. This is accompanied invariably by development, during which process tissue function switches from primarily growth to mature function, obtained through differentiation of tissue cells. The clearest example of physiological maturation is the development of muscle function and locomotory skills. Related to this are development of feeding skills and digestive function, and learning to beg for food, seek warmth and interact with siblings. Many of these changes and adaptations that result in growth are modified by environmental factors such as weather conditions, food availability, and social environment. As a consequence, the evolution of growth patterns will be shaped by the environment, because different environments require different growth strategies in order to yield the highest survival. For instance, high predation pressure might select for earlier fledging, which in turn requires a higher level of functional development, potentially at the expense of body size. The physiological control mechanisms underlying growth of individuals can constrain environmental effects on growth patterns. Because growth is such an important factor in survival, and hence the fitness of individuals, these constraints will ultimately be reflected in variation in life-history strategies. The diversification of growth patterns forms the theme of this thesis.

Below I introduce the subject of this thesis in detail, followed by the ecological background to place the study in context. Following this introduction I present the research questions discussed in each of the chapters as well as their conclusions, after which the main insights gained from the study are summarized and integrated.

Introduction to the thesis

Research questions
We investigated the allocation of limited resources and body tissues to competing demands in growing birds, and how this depends on body size. Specifically, we investigated how chicks of both smaller and larger species of shorebird resolve the conflict between rapid growth rate and the development of functional capacity. In addition, we investigated how chicks deal behaviourally with the boundaries set by their physiology and the environment, in order to maximize growth. To answer these questions we studied growth rate, energetic capacities, food availability, foraging behaviour and thermoregulatory behaviour of seven species of shorebirds ranging widely in body size. Subjects of the study were, with one exception (Japanese quail), chicks of shorebirds breeding on the subarctic tundra at Churchill, Canada.

High latitudes
At the high latitudes of the arctic, growing birds face two major environmental stressors: low ambient temperatures and a short growing season. These stressors favour different compromises between growth rate and mature function. On the one hand, a short breeding season favours rapid development, so that growth can be completed within the time that food is abundant. On the other hand, to maintain high activity levels in cold temperatures, the cold climate favours rapid development of the physiological mechanisms that generate heat, and such maturation may take place at the expense of growth rate. Adaptations to the arctic environment would involve compromises

between various aspects of organism function. Although trade-offs between competing functions are cornerstones of life-history theory (Sibly & Calow 1986, Roff 1992, Stearns 1992), they are poorly understood in growing birds.

Competing demands: growth versus function

Direct evidence that choices among alternative patterns of allocation have influenced life-history strategies, comes primarily from the resolution of conflicts between the demands of growth and reproduction (Reznick 1985, Roff 1992, Stearns 1992) or between growth rate and mature function (Ricklefs 1979, 1983, Carrier & Auriemma 1992, Herms & Matson 1992, Starck 1993).

Thermoregulatory capacity in birds depends on the functional maturity of the skeletal muscles, which are the primary source of heat production in response to cold stress in both adult and young birds (Dawson 1975, Hohtola & Stevens 1986, Olson 1994, Marjoniemi & Hohtola 1999). However, development of functional maturity also imposes constraints. The capacity of muscle to generate heat depends on certain cellular components, such as contractile proteins and pathways of energy metabolism. The development of these seems to be antagonistic to growth, because at the tissue level, many cell lines lose the ability to divide once they become differentiated. This implies that postnatal growth rate of tissues involved in locomotion is inversely related to maturation of these tissues (Ricklefs *et al.* 1994, Starck 1994, Choi & Ricklefs 1997, Starck & Ricklefs 1998, Shea *et al.* 2007). Thus, arctic environments with their low temperatures and short season are doubly stressful for young precocial birds, because both heat production and rapid growth are important.

Importance of body size

Size is an important feature in dealing with cold and it strongly influences development time. Perhaps most importantly, it influences the capacity for heat retention. Small chicks have an unfavourable surface-to-volume ratio and lose heat rapidly to the environment, compared to larger chicks that are better able to maintain their body heat. Larger chicks however, although their capacity for heat retention is higher, exhibit lower growth rates and thus need more time to complete growth. Consequently, for small species the low ambient temperatures in the arctic become limiting, whereas for larger species the short season becomes limiting. It has been suggested that this explains why the most northerly distributed scolopacids are of intermediate body size (Godfrey 1966, Hayman *et al.* 1986, Schekkerman *et al.* 2003). These species apparently can resist cooling sufficiently, while they still grow rapidly enough to complete growth in the short season. Investigating growth, behaviour and performance in a range of small, intermediate and large species will help us to understand the physiological requirements and limitations for existence under arctic conditions.

Shorebirds

Shorebirds are an excellent group to study how individual chicks respond developmentally to the cold and short arctic season. A large number of species nest at high latitudes, and local nesting densities are high in comparison to, for instance, most altricial species (Järvinen & Väisänen 1978, Chernov 1985, Troy 1996). In addition, shorebirds come in a large range of sizes: in species occurring at the Churchill study site, neonatal mass ranges from 4 g in the least sandpiper to 33 g in the whimbrel. Being precocial, shorebird chicks leave the nest soon after hatching to forage by themselves, but, as they are not yet homeothermic, they lose body heat while foraging and must be rewarmed by their parents at regular intervals. Because of the active foraging of precocial chicks, a large fraction of their resources is allocated to functions other than growth such as foraging and ther-

Chicks of least sandpiper (left) and whimbrel (right) of just a few days old. These were the smallest and the largest species that were studied. Photos K. Krijgsveld.

moregulation, compared to more altricial chicks. To deal with the highly varying and often unfavourable environmental conditions, the ability to adjust growth patterns to demand is an important mechanism for increasing chances of survival. Various studies indicate that precocial chicks show a high flexibility in developmental response (Schew 1998, van der Ziel & Visser 2001, Starck & Rahmaan 2003). The way in which birds cope with such environmental stresses may ultimately determine the northern extension of their breeding ranges (table 1.1).

Table 1.1. Some characteristics of the seven species of shorebird studied in this thesis. Body masses from own observations and literature (see chapter 2). Time needed to fly is crudely estimated (Jehl 2004, own observations). Breeding range is the approximate breeding range of birds in North America (Godfrey 1966, Hayman *et al.* 1986).

species	body mass (g) neonate-adult	time to fly (d)	breeding range (°N)	latin name	Dutch name
least sandpiper	4 – 21	16	46–71	*Calidris minutilla*	kleinste strandloper
dunlin	8 – 50	16	54–72	*Calidris alpina*	bonte strandloper
lesser yellowlegs	11 – 81		51–70	*Tringa flavipes*	kleine geelpootruiter
short-billed dowitcher	12 – 113	21	53–62	*Limnodromus griseus*	kleine grijze snip
American golden plover	18 – 145	24	57–75	*Pluvialis dominica*	Am. goudplevier
Hudsonian godwit	25 – 255		54–69	*Limosa haemastica*	rode grutto
whimbrel	33 – 380	27	54–70*	*Numenius phaeopus*	regenwulp

*Possibly up to 73°N at Banks Island

Eggs of the shorebird species studied in this thesis. Clockwise starting with the largest egg: whimbrel, Hudsonian godwit, short-billed dowitcher (hatching), lesser yellowlegs, dunlin, least sandpiper. Photo K. Krijgsveld.

Although conditions become more limiting for chicks at more northerly locations, we chose to study shorebird growth at a moderate latitude, on the subarctic tundra at Churchill, Canada (fig. 1.1). Here, both small and large species breed in high numbers, in contrast to more northerly locations, allowing comparisons between differently sized species within one location. Although these birds do not live in the most extreme environment and thus may not operate at maximum capacity, the local variation in environmental conditions and the related variation in physiological and behavioural performance should allow us to elucidate constraints.

We focused on seven species of shorebirds. Species were, from small to large: least sandpiper, dunlin, lesser yellowlegs, short-billed dowitcher, American golden plover, Hudsonian godwit and whimbrel (table 1.1). These species belong to three subfamilies of the family of Scolopacidae, except for the plover which belongs to the family of Charadriidae. Precocial chicks of Japanese quail Coturnix c. japonica (Galliformes: Phasianidae) were used in additional laboratory experiments.

Study area

The field studies reported here were carried out on the tundra near Churchill, Manitoba, in Canada (fig. 1.1). The area is situated on the western shore of the Hudson Bay, at 58°45'N, 94°04'W. It qualifies as a subarctic region, and is situated at approximately the same latitude as Oslo. The land falls out eastward into the Bay here, and the shoreline thus runs east-west rather than north-south. Because of this, the area and thus the chicks are exposed to a wide range of environmental conditions (fig. 1.2). When the wind blows from the north, from across the Hudson Bay, temperatures can become arctic, while they are considerably higher when the wind blows from the south across the American continent. These conditions have created a zone where tundra habitat has developed from

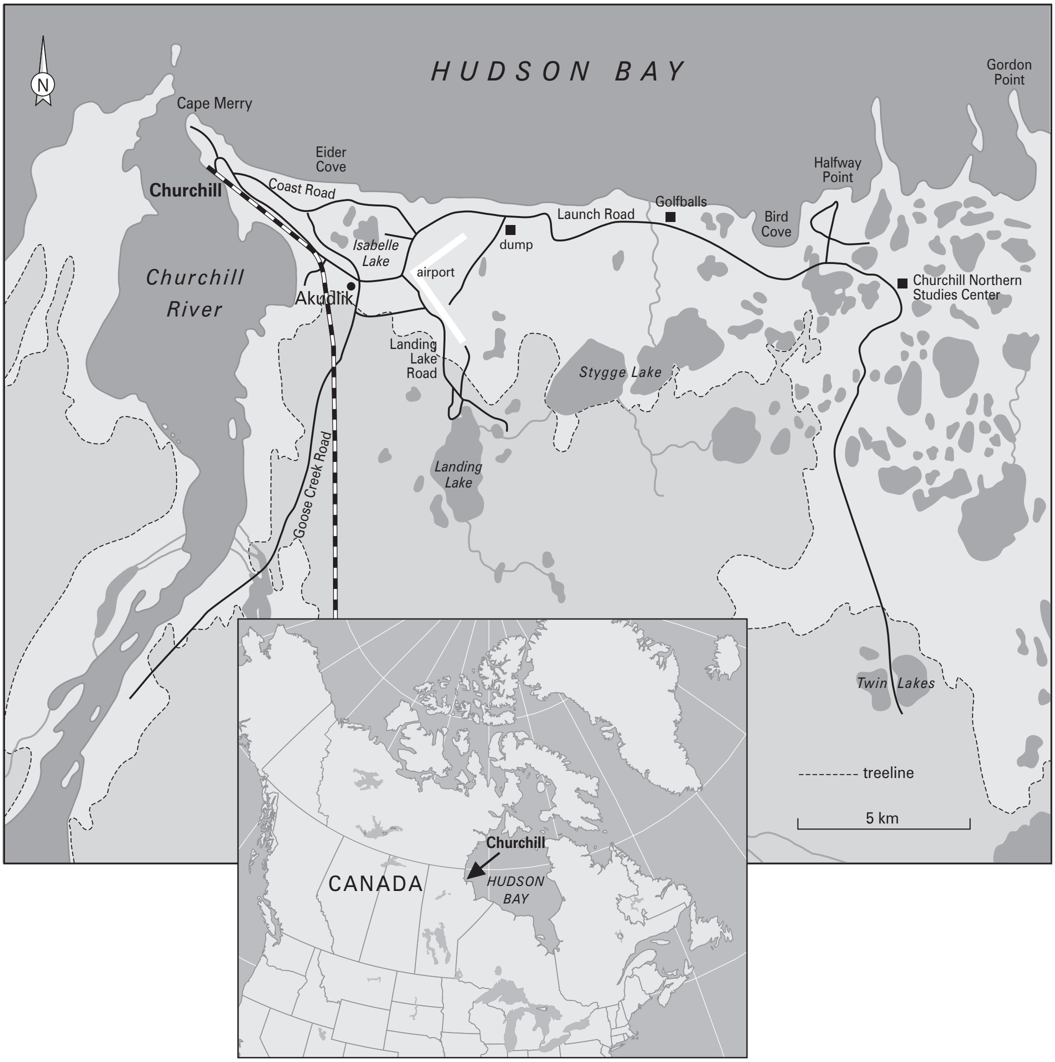

Figure 1.1. Location of Churchill on the Hudson Bay in Canada, and the research area at Churchill.

the shore to ca. 20 km inland. Further south, the exposure to cold northerly winds is less, and the habitat gradually changes into boreal forest. It is one of the southernmost tundra habitats in Canada and for many of the shorebirds attracted to the area it is the southernmost breeding range. In midsummer, the sun rises 3:20 and sets at 22:00 h CDT, with a long period of civil twilight, from 1:45 and until 23:30. Mean temperature in July was 12°C on average between 1943 and 2000 and 13°C during the study years (1994–1998). Especially 1996 and 1997 were warm summers with an average July-temperature of 14.1 and 14.7°C, respectively. Coldest of the study years was 1995, with an average July-temperature of 11.7°C (data from the Commercial Weather Services, Environment Canada, Winnipeg, Canada).

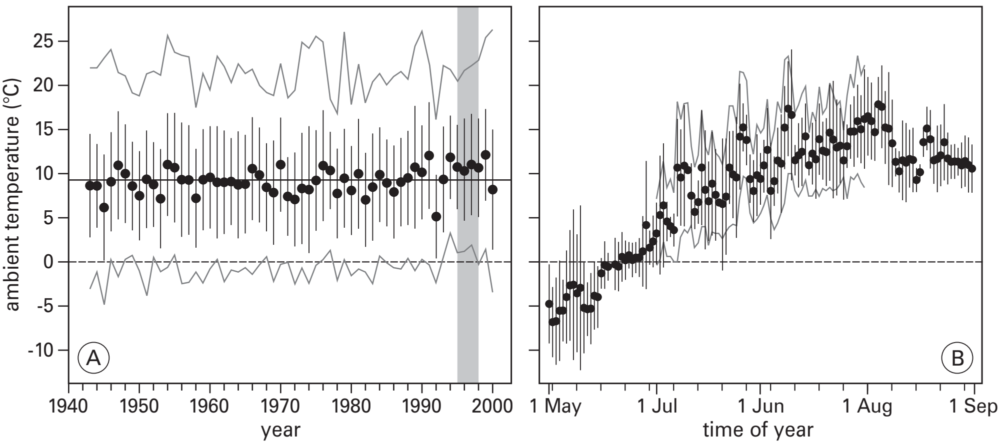

Figure 1.2. Overview of ambient temperatures in Churchill. (A) Temperature in July (the period that chicks are growing) averaged over the period 1940 through 2000, with standard deviations and minimum and maximum (grey lines). The study period is indicated in grey. (B) Temperatures during the breeding season from 1 May through the end of August, averaged over the study years 1994-98. Shown are daily averages (averaged over years) with standard deviations. Average daily minimum and maximum are shown as well for June and July (grey lines). Source: Commercial Weather Services, Environment Canada, Winnipeg, Canada.

Shorebird breeding ecology

Of the shorebirds of the American continent, large numbers breed on the tundras of northern Canada. In the Churchill area 15 species of shorebirds occur, at slightly more than 0.1 pair of shorebird / ha in 1997, and predominated by American golden plover, whimbrel, semi-palmated plover and dunlin (Jehl & Lin 1997). For example, breeding density of dunlin can be up to 1 pair / ha in good areas (Jehl 2004) and average breeding density of whimbrel was 0.006 pair/ha in 2007/08 (Ballantyne & Nol 2011). The birds winter in Central and South America as far as Cape Horn, and in spring they migrate north to their breeding grounds (Hayman *et al.* 1986). The period that conditions are suitable for breeding is short, and the various stages of breeding rapidly follow each other. The adults arrive by the end of May and find a breeding territory and a mate. Each species requires its own characteristic breeding habitat. Site fidelity is high, with birds often returning to the same nest cup (Jehl 2004). The clutch almost invariably consists of four large eggs that hatch by the beginning of July when the snow has melted and food is becoming more abundant. The four eggs hatch more or less simultaneously, within approximately one or occasionally two days. Chicks of smaller species take ca. 16 days to complete growth, whereas those of larger species such as the whimbrel take longer, close to 30 days (table 1.1). From mid-July into August, when food is becoming less abundant and chicks have grown, the adults start to migrate south again, followed some time thereafter by the juveniles (up to early September, Jehl 2004).

After hatching, the family may either remain in the nesting area or, led by the adults, move to more profitable feeding areas where more food is available or where fewer predators occur. Within this territory or feeding area the chicks search for their own food (Hammond & Pearson 1994). When chicks are still young or when the weather is cold, they forage close to the adult, but as they grow older and in warmer weather, they move further away from the adult. In all species studied in this thesis, both adults remain with the chicks until they are capable of flight. The adults remain

Golden plover chicks in their nest. Temperature-sensitive transmitters are attached to two of the chicks. Photo K. Krijgsveld.

within their breeding territories to brood their chicks as well as to guard the eggs and chicks from the ample predators, such as northern harriers, short-eared and snowy owls, parasitic jaegers, common ravens and Arctic foxes. The adults forage within this territory or, as in e.g. the American golden plovers, take turns in guarding and brooding the chicks, while the other leaves to forage somewhere outside the territory.

At the end of a foraging bout, the chicks and the incubating adult move closer together and increase their exchange of calls. The adult then selects a suitable brooding site, hunkers down and invites the chicks to brood underneath him or her by calling and nodding while pointing its bill down. There is some discussion as to who initiates brooding bouts, the adults or the chicks (Johnson *et al.* 2008). Usually, the process runs so smoothly that it is hard to detect who initiates the brooding bout, adult or chick. When the weather is cold, chicks are seen approaching the adult more often, following it and begging to be brooded before the adult actually sits down to brood. The other way round is also observed, especially during warmer days, when the adult can be seen calling for the chicks and sitting down to brood while none of the chicks approaches and all continue foraging (own observations). All chicks of a family brood and forage simultaneously. To reduce exposure to the cold, the youngest chick starts foraging last and returns to the adult to be rewarmed first, especially in the first days after hatching and during adverse weather (own observations, Hussell & Page 1976).

Research questions and summary of results

Part 1 – Setting: chick growth rates and food availability

To understand the results regarding physiology and behaviour of the shorebird chicks, we first present two basal aspects of chick life: chick growth rates and food abundance. These two aspects form the background against which the subsequent chapters are built, and therefore are presented first.

Growth rates and the effect of body size - chapter 2

Background – Size of chicks defines the boundaries for an array of behaviours and physiological capacities, and as such are essential parameters when studying time budgets and physiological capacities of chicks. For example, the surface-to-volume ratio of a chick determines (among others) how fast heat is lost to the environment, and therefore a larger body size results in higher heat retention (Visser & Ricklefs 1993a,b; Bakken *et al.* 2002). Also capacity for heat production is closely related to body size (Weathers 1992). In turn, the capacities for heat retention and heat production determine to a large extent how rapidly a chick cools and thus, for instance, how long it can continue to forage when temperatures are below the thermoneutral zone. Indirectly, the growth rate of a chick is thus an important parameter when studying behaviour and physiology of chicks. We studied growth rate in relation to variation in body size between species, allowing us to relate behavioural and physiological performance of the various species to their size and growth rate.

Question & approach – We studied the differences in growth rates of chicks of seven species of shorebirds. These species cover a large range in body size, from 4 g to as much as 33 g neonatal body mass, an 8-fold difference (table 1.1). Growth was measured from hatching through to fledging age, three to four weeks later. Species were, from small to large, least sandpiper *Calidris minutilla*, dunlin *C. alpina*, lesser yellowlegs *Tringa flavipes*, short-billed dowitcher *Limnodromus griseus*, American golden plover *Pluvialis dominica*, Hudsonian godwit *Limosa haemastica* and whimbrel *Numenius phaeopus*. Birds were all raised under laboratory conditions, but were placed in outdoor enclosures for several hours almost daily to promote natural locomotory and thermoregulatory behaviour. Food, water and heat were provided *ad lib*.

Results – Our results show, firstly, that the smaller species grew faster than the larger species, when calculated as a proportion of their asymptotic size. This was true for increase in both body mass and the primary locomotory organs, legs and wings, as well as the bill (fig. 1.3) (naturally, absolute growth rate was much higher in the larger than in the smaller species). This result is in line with the growth patterns found when comparing species on a larger taxonomic scale (Ricklefs 1968) and shows that it also applies within the group of shorebirds. This further implies that a trade-off between growth rate and mature function also could apply within this group of shorebird species. Because of their larger size, the larger species were found to require a longer period of time to complete growth than the smaller species. However, growth rate of the two largest species, Hudsonian godwit and whimbrel, was high for their size, in comparison to other similarly sized shorebird species, while growth of the intermediate sized species (yellowlegs, dowitcher and plover) was slow for their size.

Interpretation – We hypothesize that the two larger species, which lose relatively little heat to their environment, invest relatively little in functional capacity and more in growth (this is discussed further in chapters 4&5). Thus they may shorten the time needed to reach adult size, which is crucial for larger birds growing up in arctic areas with brief summer seasons. In intermediate sized species,

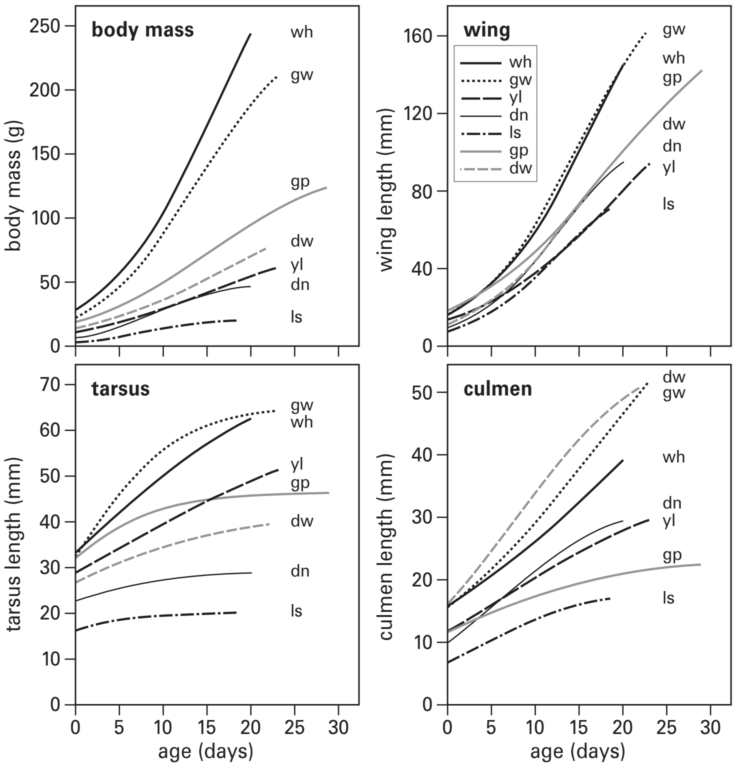

Figure 1.3. Growth rate of seven species of shorebird chicks, shown as a function of adult body mass, and of adult or fledging (for tarsus) size of wing, tarsus, and culmen. Shown are growth constant K (left panels), which is a measure for growth rate, and the inflection point ti (right panels), which is a measure for the time needed to complete growth. Values of K and ti based on logistic curve fitting. Species include least sandpiper, dunlin, Hudsonian godwit and whimbrel (black symbols), lesser yellowlegs (grey symbols), short-billed dowitcher and American golden plover (white symbols). Linear regression for all species combined. Chicks of smaller species had higher growth rates (NS) and completed growth sooner than chicks of larger species (same as fig. 2.2).

the need for rapid growth may possibly be relaxed because time needed to complete growth is less than in larger species, while at the same time the rate of heat loss is less than in smaller species. Previous research by Tjørve *et al.* (2009) has indeed shown that growth rates were higher in shorebird species growing in colder ambient conditions as well as in areas with shorter breeding seasons. These findings suggest that growth rates may be under selective pressure, and consequently that physiological processes in the chicks, such as growth rate, metabolic rate and muscle function, may be adjusted to maximize chances of survival.

Food availability – chapter 3

Background – The availability of food not only affects foraging behaviour of the chicks, but also their growth and energy expenditure. For instance, Tulp *et al.* (2004) showed that growth rate of little stints was related to food abundance on the tundra in Taimyr. Food availability can thus play a large role in developmental processes of the chicks.

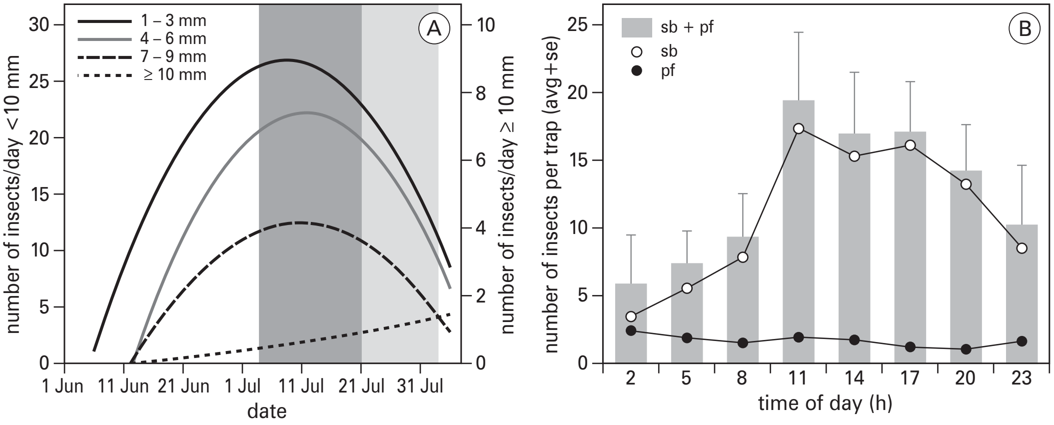

Figure 1.4. Seasonal and diurnal patterns in food availability. (A) Seasonal variation in abundance between smaller and larger species of arthropods caught on sticky boards, shown as fitted quadratic functions of sample data. Grey bars: mean chick hatching date to early age of sustained flight of small shorebird species (dark grey) up to later age of sustained flight of larger shorebird species (light grey). Vertical dashed line: mean onset of incubation. Larger arthropod species emerged later in the season, had a shorter peak and a lower abundance. Peak in food abundance coincided with the main growing period of shorebird chicks (modified from fig. 3.4). (B)Diurnal pattern in arthropod abundance. Number from sticky boards and pitfalls combined (bars, ± se) as well as separately (circles). Only the 02:00 sample was collected during hours of darkness (midsummer twilight: 23:30–1:45 CDT). Highest numbers were caught at 11:00 h. (same as fig. 3.5).

Question & approach – We investigated how food availability varied through the season and with the time of day, as well as with weather conditions. Food of shorebird chicks covers of a large variety of invertebrate taxa, but mainly consists of arthropods (Holmes & Pitelka 1968, Baker 1977, Skagen & Oman 1996). We sampled arthropods in two vegetation types, one being wetter vegetation with predominantly sedges, and one being drier vegetation with lichens, berries and small willows. Traps consisted of pitfall traps to catch ground-dwelling insects and sticky boards to catch flying insects.

Results and interpretation – In total, we collected 38 families of arthropods in 12 orders. The majority of arthropods were Diptera (flies, 78% of the total number caught), followed by mosquitoes and chironomids. An average of 49 arthropods were caught per trap per day, with a dry biomass of 114 mg, but variation was large. Numbers were similar to those reported in other arctic studies, although they were high compared to studies at both lower and higher latitudes (MacLean & Pitelka 1971, Danks 1999, Tulp & Schekkerman 2008). These high numbers suggest that feeding conditions for shorebird chicks were good in comparison with other areas.

The availability pattern of the different arthropod species was in synchrony with the food demand of the chicks (fig. 1.4). The number of arthropods peaked between the end of June and the end of July, while the majority of chicks hatch late June - early July, and need between two and four weeks to fledge, depending on size (table 1.1). The smallest arthropod species, which are particularly suitable prey for young chicks (Schekkerman & Boele 2007), reached maximum numbers earliest in the season, around the mean hatching date of the chicks. The larger arthropods peaked later in the season, around mid to late July, in line with the higher energy demands of larger chicks, which are able to feed on larger prey species. The seasonal pattern in numbers reflected the differences in latitude. At Barrow, which lies further north, the arthropods peaked for a much briefer period (MacLean

& Pitelka 1971). There, arthropods were available for no more than ca. 20 days, while at Churchill they were available for ca. 35 days.

Prey availability showed consistent patterns throughout the day. Numbers (and mass) of arthropods were considerably higher during daytime than at night (fig. 1.4). Numbers caught increased in the early morning hours to a peak at ca. 11:00 CDT. Numbers decreased again in the late afternoon or early evening (17:00–20:00). This pattern was reflected in the foraging behaviour of free-living American golden plover chicks. Their foraging bouts were longest in the late morning, consistent with highest levels of food availability.

Weather conditions also affected the numbers of arthropods caught. Numbers decreased with lower ambient temperatures and with increasing wind speeds. This relation partly explains the diurnal pattern in prey availability, because temperature was highest during mid-day hours, and wind speeds were lower in the morning and evening than in the afternoon. Schekkerman & Boele (2008) have shown that ingestion rate of chicks is lower with higher wind speeds and higher ambient temperatures. The low wind speeds and low ambient temperatures during the early morning hours might therefore increase the accessibility of individual arthropods, making foraging more favourable.

Part 2 – Physiological adaptations: growth rate versus functional maturity

In this part we investigate how chick growth rate relates to functional maturity of the tissue, and whether the two are inversely correlated. For this purpose we studied both muscular performance (catabolic capacity) and daily energy expenditure in chicks varying in size.

Catabolic capacity and muscle growth rates indicate high developmental flexibility – chapter 4

Background – Newly hatched precocial chicks must grow rapidly to achieve independence before the end of the short arctic growing season. A rapid growth rate may however conflict with the development of functional capacity (Ricklefs *et al.* 1994) required to walk and to generate heat. Because of the allometric scaling of thermal relationships, this trade-off might be resolved differently in small and large species.

Question & approach – We hypothesized that the development of catabolic capacity is delayed in faster-growing muscles and to test this, we assessed growth rate (mass) and functional capacity in leg and pectoral (*i.e.* flight) muscles of chicks of the smaller dunlin and the larger whimbrel. Functional capacity was assessed by measuring the activity of three enzymes that function as regulatory, non-equilibrium enzymes in the major catabolic pathways; thus providing an index for aerobic capacity (citrate synthase CS), glycolytic capacity (pyruvate kinase PK) and capacity for lipid metabolism (L-3-hydroxyacyl-CoA-dehydrogenase HD) (Marsh & Wickler 1982, Newsholme & Crabtree 1986, Olson 1990). Simply put, the activity of these enzymes determines the maximum amount of energy that can be generated in the muscle tissue.

Results – Growth rate varied between species and tissues. The smaller dunlin chicks showed a more rapid (relative) growth of body mass compared to whimbrel chicks. Muscle growth was higher in the leg than in the pectoral muscles in both dunlin and whimbrel, consistent with rapid development of the leg, which is needed for locomotion and early thermoregulation. Pectoral muscles of dunlin chicks grew much faster than those of whimbrel, correlating with the earlier development of flight in the dunlin. Leg muscles of whimbrel chicks however grew faster than those of dunlin. Summarizing muscle growth rate: whimbrel-leg ≥ dunlin-leg > dunlin-pecs > whimbrel-pecs.

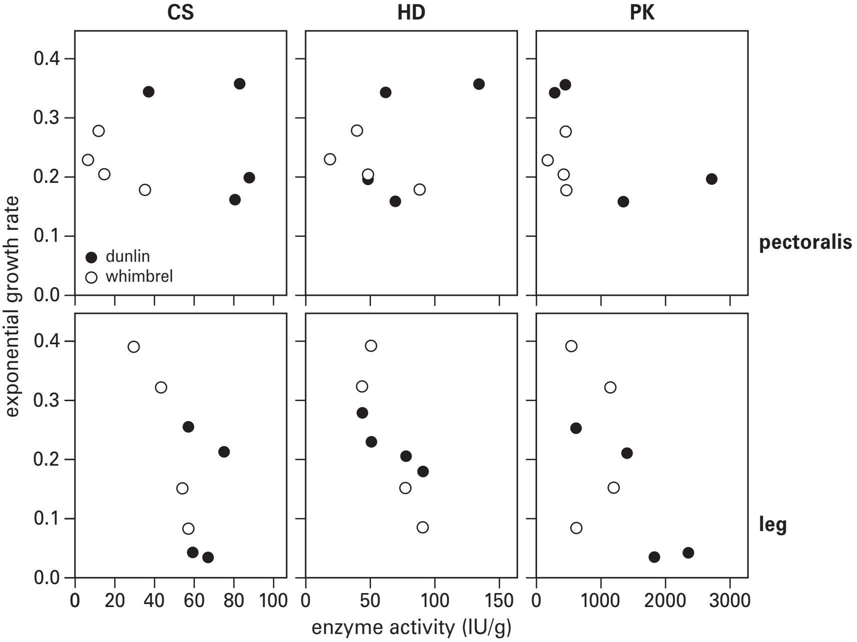

Figure 1.5. Exponential growth rate in relation to the activity of citrate synthase (CS), hydroxyacyl-CoA-dehydrogenase (HD), and pyruvate kinase (PK) in pectoral and leg muscles of dunlin and whimbrel. Especially in the leg muscles, the significantly negative correlation between growth rate and functional capacity supports the theory of a trade-off between the two. Note the high capacity for glycolysis (PK-activity) (same as fig. 4.6).

Catabolic capacities in the muscles of the two precocial species were high compared to levels of altricial species that grow much faster than precocial chicks. This is in line with the hypothesis that growth rate is negatively correlated with development of mature function. Especially glycolytic capacity (PK) played an important role in heat production in precocial chicks compared to altricial chicks, much more so than aerobic capacity (CS). Catabolic capacities of dunlin and whimbrel chicks were generally higher in the leg muscles than in the pectoral muscles and were close to adult levels. Leg muscles are needed for locomotion shortly after hatching, and also make up the bulk of the thermoregulatory capacity of the chick early in development. Summarizing muscle function at young ages: dunlin-leg ≥ whimbrel-leg > dunlin-pecs ≥ whimbrel-pecs; or leg > pec and dunlin > whimbrel at young ages.

Interpretation – Exponential growth rate and catabolic capacity were negatively correlated, especially in the leg muscles and for CS activity, which matches our expectations regarding a trade-off between growth rate and functional maturity. However, differences in levels of enzyme activities between the two species and between the leg and pectoral muscles indicate that processes other than this trade-off play important roles in determining catabolic capacity and growth rate. Dunlin chicks for example, that grow faster, generally were found to also have higher levels of enzyme activities than whimbrel chicks at any given age. This was especially the case for pectoral muscles, while leg muscles of the two species had similar capacities relative to body mass (fig. 1.5). This indicated that whereas dunlin chicks rely more on catabolic capacity to generate heat, whimbrel chicks with their larger mass can rely much more on heat retention to maintain their body temperature instead of increased function. This may explain why the whimbrel chick is homeothermic at only three days of age, while the dunlin does not achieve homeothermy until eight days of age (Visser 1993b). The negative correlation between catabolic capacity and growth rate in the leg muscles, which was absent in the pectoral muscles, may reflect the importance of locomotion and thermoregulatory function early in development. Overall, larger and smaller species may adopt different strategies of growth and tissue maturation. These results partially contradict the growth rate – mature function trade-off, and suggests that at least chicks of precocial species have considerable latitude to modify this relationship.

High daily energy expenditure combined with high growth rates in small chicks – chapter 5

Background – Because of their precocial mode of development, shorebird chicks operate at a high level of energy expenditure: this is required for locomotion and thermoregulation, particularly in cold environments at high latitudes. Body size plays an important role in the level of energy expenditure of the chick, because smaller chicks have a higher mass-specific thermal conductance and thus lose body heat more rapidly (Weathers 1992, Visser & Ricklefs 1993a,b). The measurements of catabolic capacity (chapter 4) indeed showed that the smaller species had higher levels of functional maturity. These results suggested that compared to chicks of larger species, chicks of smaller species could exhibit proportionately higher mass-specific daily energy expenditure (DEE) when they are foraging and being exposed to wind and low temperatures under semi-natural conditions.

Question & approach – To investigate the effect of body size on DEE of precocial chicks under semi-natural conditions where they are foraging and are exposed to environmental conditions, we measured the levels of DEE in chicks of five shorebird species that were kept in outside enclosures on the sub-arctic tundra. DEE was measured using doubly labelled water at various stages of the growth period. Species were least sandpiper *Calidris minutilla*, dunlin *Calidris alpina*, lesser yellowlegs *Tringa flavipes*, Hudsonian godwit *Limosa haemastica*, and whimbrel *Numenius phaeopus*, which ranged in neonatal mass from 4 to 33 g respectively. We also quantified the effect of weather conditions on the energy budget of chicks, in order to establish the impact cold arctic weather has on their time and energy budgets.

Results – We found no significant effect of ambient temperature on DEE, although higher wind speeds did result in slightly higher DEE levels. An explanation for this lack of effect of temperature on DEE may be that the amount of heat produced by locomotion was sufficient to sustain thermoregulation under the local environmental circumstances in Churchill (mean ambient temperature for July of 12ºC). A further explanation is that when ambient temperatures were low, chicks spent more time brooding and less time foraging (chapters 6&7). Brooding reduces energy expenditure at low temperatures (chapter 7), which counters the tendency to increase thermogenesis in response to cold.

Levels of DEE of all five species of shorebird chicks were high compared to those of altricial chicks from hatching onward (fig. 1.6). DEE levels at the youngest ages were well above levels of resting metabolic rate (RMR) of neonate shorebirds, and were proportionately much higher than that of neonate altricial chicks – (chapter 5). DEE increased rapidly as chicks grew older and larger, as indicated by the high allometric scaling exponent ($b = 1.38$). Compared to altricial species, precocial chicks invest a relatively large proportion of their resources in development of their muscles to increase locomotory and thermoregulatory function (Starck & Ricklefs 1998). Thus, it is not surprising that their metabolic function developed at a high rate. However, although DEE levels were initially high in precocial chicks, reflecting the high costs for locomotion and thermoregulation, development of DEE did not subsequently increase more rapidly than in more altricial species. Smaller species had higher DEE levels than larger species for a given body mass. This is in line with

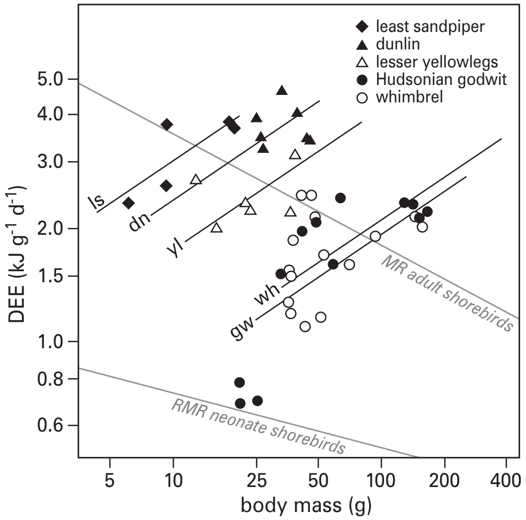

Figure 1.6. Daily energy expenditure per gram body mass as a function of body mass, in chicks of five species of shorebirds representing a wide range in body size. Regression lines are plotted as solid lines, using the common slope for all five species (b = 0.38), & are extended to cover the full range in body mass from neonate to adult. Dotted lines depict the resting metabolic rate of neonatal shorebird chicks (Visser & Ricklefs 1993b) and the metabolic rate of adult shorebirds exposed to 10°C (Kersten & Piersma 1987). Chicks of smaller species, although growing faster, also have a higher mass-specific daily energy expenditure than chicks of larger species (same as fig. 5.2).

the generally higher metabolic intensity of smaller species (e.g. King & Farner 1961) and the fact that, for a given mass, chicks of smaller species are closer to adult size than those of larger species. DEE was similar to cold-induced peak metabolic rates achieved by shivering thermogenesis. Because chicks were motionless during laboratory metabolism measurements, the relatively high level of DEE compared to these metabolic rates suggests that locomotion produces substantial amounts of heat, similar to those produced through shivering.

Interpretation – Chicks of small shorebird species not only performed at a relatively high energetic level but also grew at a high rate, whereas chicks of larger species performed at a relatively lower level and grew less quickly. This positive correlation between mature function and growth rate contradicts a trade-off between growth rate and mature function, similar to the results found for catabolic capacity (chapter 4), and suggests that shorebird chicks can modify the relationship between growth rate and mature function considerably.

Summarizing chapters 4 & 5, chicks of small arctic sandpipers, which are among the smallest homeotherms, are remarkable for maintaining high levels of metabolic activity while simultaneously growing rapidly. The chicks of larger species also grow rapidly to achieve adult size during the brief arctic growing season, but their lower thermal conductance and heat loss results in a lower mass-specific daily energy expenditure. Therefore, although locomotion contributes significantly to heat production, the higher daily energy expenditure per gram of the chicks of smaller species is more closely related to thermogenic considerations than to foraging. Thus, smaller species are likely to be more sensitive to variation in temperature and wind speed than larger species, and these environmental conditions undoubtedly limit the northern distributions of these species.

Part 3 – Behavioural adaptations: foraging behaviour and body temperatures

In this part we investigate how the chicks adapt behaviourally to the changing and often adverse weather conditions, and how physiological processes are adjusted to enable foraging under these conditions. One of the key variables here turned out to be body temperature of the chicks, which determines foraging behaviour to a large extent.

Foraging behaviour and body temperatures of golden plover chicks – chapter 6

Background – Given the physiological framework of catabolic and metabolic function, as summarized above, the next question is how the chicks deal behaviourally with the boundaries set by their physiology. Precocial shorebird chicks lose body heat while foraging, and consequently must be brooded by a parent at regular intervals. Their temporal behaviour patterns are therefore strongly dependent on food availability and environmental conditions that affect the heat balance such as ambient temperature and wind speed. The extent to which these conditions affect foraging time is largely determined by the physiological capacities of the chick, such as thermal conductance and metabolic rate. During foraging, chicks cool, eventually resulting in reduced locomotory capabilities as well as reduced digestive rate and efficiency (Kleiber & Dougherty 1934, Osbaldiston 1966, Pedersen & Steen 1979, Chappell 1980). To maintain body heat, metabolic rate increases while cooling, up to a maximum level, after which both metabolism and body temperature fall rapidly (Ricklefs & Williams 2003). Foraging bouts therefore should terminate when the energetic profits (food intake) are outweighed by the energetic costs (heat loss and increased metabolism). This balance defines the duration of foraging bouts, and ultimately determines the northern limits to the breeding distribution.

Question & approach – To investigate how the physiological capacities of precocial chicks determine the time available for foraging, we studied time budgets and body temperatures (measured rectally or with implanted temperature-sensitive radio transmitters) of free-living families of American golden plovers *Pluvialis americana* as well as golden plover chicks foraging under seminatural conditions in an outdoor enclosure. Chicks in the enclosure had access to a box with an infra-red brooding lamp where they could rewarm. Food and water was provided ad lib because natural food items were limited and quickly depleted in the enclosure.

Results – American golden plover chicks foraged between 3:00 and 23:00, and thus a maximum of 20 h was available for foraging per day. The percentage of that time spent foraging increased with increasing ambient temperatures as well as with age, through an increase in the length of foraging bouts (fig. 1.7). As ambient temperatures decreased, foraging bouts were shorter and chicks alternated between brooding and foraging more often. Foraging bouts were significantly longer in the late morning hours (06:00–11:00h) than during other parts of the day, regardless of chick age and ambient temperature. This increase was related to a combination of factors. Insect availability increased during that time of day to reach peak numbers at 11:00 and apparently made foraging more profitable, especially after the night-time fasting period and the cold early-morning hours (chapter 3).

Chicks experienced relatively warm summers in our study years. As a result, the time available for foraging in our study was probably higher than during typical summers (for example, 60–65% of the daylight period versus only 40% during typical summers, for a 3-d-old chick). Ambient temperatures varied strongly however, generating large fluctuations in available foraging time. Churchill is at the southernmost edge of the distribution of breeding American golden plovers. Further north, average ambient temperatures are lower, thus further restricting foraging time, but conditions there are apparently still favourable enough for golden plover chicks to fledge successfully.

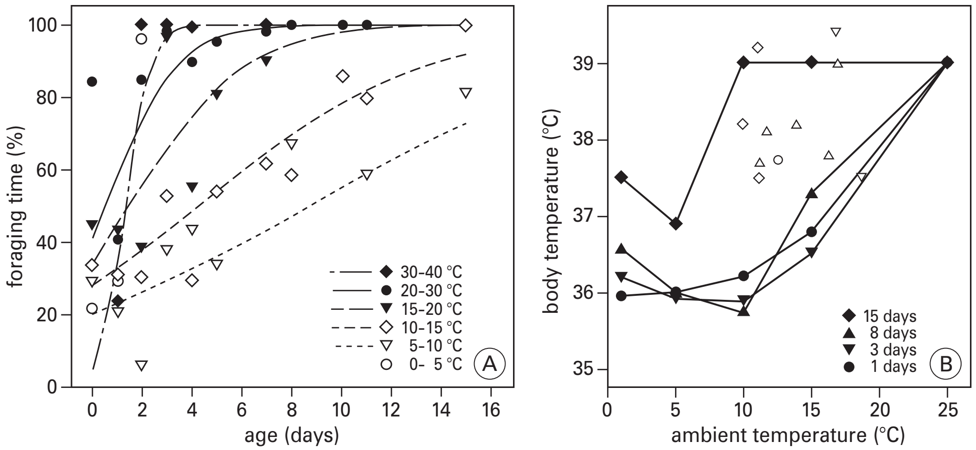

Figure 1.7. (A) Time spent foraging by free-living chicks of American golden plover, in relation to age of the chick and ambient temperature. Chicks spent more time foraging when ambient temperatures were higher. Foraging time increased rapidly with increasing age, and varied largely. (B) body temperatures of American golden plover chicks of various ages at the end of a foraging bout. At all ages, chicks maintained high body temperatures and ended a foraging bout and returned to the parent to be rewarmed when body temperatures dropped below 35.5°C, rather than continuing to forage (same as figs. 6.3 & 6.7).

Body temperatures of foraging chicks were found to be lower under colder environmental conditions. In young chicks, body temperature showed a large variation, but this range decreased when chicks grew older, until at six days of age homeothermy was reached and body temperature was more or less stable. Even at younger ages, body temperatures were never lower than 35.5°C at the end of a foraging bout when chicks returned to the parent to be rewarmed (fig. 1.7). This was established both by direct measurements of body temperatures at the end of foraging bouts of chicks in enclosures, and by model estimates based on the cooling rates and the average foraging bout lengths of free-living chicks.

Interpretation – Overall, the relatively moderate temperatures at Churchill did not appear to limit foraging time of golden plover chicks and postnatal development was relatively unaffected by the local climate. This follows from our finding that foraging bouts varied widely for a specific age or ambient temperature, indicating that environmental conditions were not the sole determinant of time budgets of the chicks. In addition, the observed increase in foraging bout length during late morning suggests that chicks were able to lengthen foraging bouts in relation to factors other than ambient temperature. Finally, growth rate of free-living chicks was at least as high as that of chicks raised in the lab, suggesting that foraging time was sufficient to satisfy food requirements.

Our findings on body temperatures are in contrast with the pervasive notion that precocial chicks use their ability to remain active at lower body temperatures to prolong foraging bouts (Norton 1973, Myhre & Steen 1979, Chappell 1980, Visser 1993a).

Effect of low temperatures on foraging behaviour and physiology – chapter 7

Background – Precocial chicks in the arctic are constrained by the brevity of the breeding season and/or the low environmental temperatures. Under cold environmental conditions, the balance between investment in growth on the one hand and thermoregulatory and locomotory function on

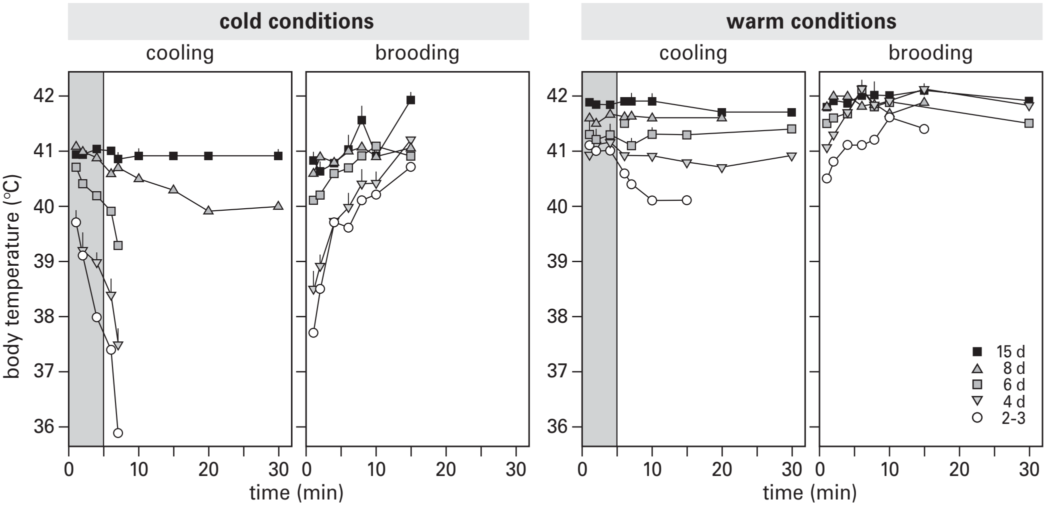

Figure 1.8. Body temperatures (mean ± se) of chicks of various ages, during cooling (left panels) and subsequent rewarming (right panels) sessions, plotted as a function of exposure time. Left block show cold-exposed chicks, right block chicks under warm conditions. Voluntary cooling bouts of cold-exposed chicks ended at 5 minutes on average (shaded area), indicating that, similar to free-living golden plover chicks, quail chicks maintained relatively high body temperatures during foraging (same as fig. 7.4).

the other hand may shift, as thermoregulatory function becomes more important. As was established for foraging golden plover chicks (chapter 6), a chick can compensate for deteriorated environmental conditions by adjusting its behaviour. Furthermore, our studies on catabolic capacity (chapter 4) and daily energy expenditure (chapter 5) indicate that shorebird chicks can modify the relationship between growth rate and mature function considerably, thus contradicting a trade-off between growth rate and mature function.

Question & approach – To investigate experimentally how precocial chicks adjust their behaviour to cope with low ambient temperatures, and to determine the flexibility in the balance between investment in growth rate and mature function, we exposed captive Japanese quail chicks *Coturnix c. japonica* to different ambient temperatures. Newly hatched chicks were raised at either high or relatively low temperature (24 vs. 7°C), and both groups had *ad lib* access to a heat source (infra-red brooding lamp), food and water. In both groups we measured time budgets, body temperatures, food intake and foraging efficiency, energy expenditure and growth rate.

Results – Foraging patterns of quail chicks were roughly the same as those of free-living golden plovers. The percentage of time spent away from the heat source was higher under warmer conditions, and increased with age. Foraging bouts were shorter under cold conditions than in a warm environment.

With regard to physiology, the patterns we found in body temperatures were also very similar to those of golden plover chicks. Body temperatures decreased faster and were lower under cold conditions than in a warm environment. More importantly, chicks also maintained high body temperatures and ended foraging bouts at body temperatures above 37°C (fig. 1.8). Cold-exposed chicks developed a higher foraging efficiency (food intake per time spent on actual foraging) and a higher total food intake, to match a higher energy expenditure.

The joint development of metabolic rate and body size showed that at all ages the increase in growth rate lagged behind the increase in resting metabolic rate. Metabolic rate was similar in the cold and the warm environment in chicks of a week old, but subsequently increased more rapidly in cold-exposed chicks and was significantly higher in this group from two weeks of age onward. Initially, growth rate of cold-exposed chicks was reduced compared to that of chicks exposed to warm temperatures, but growth rate increased as chicks grew older to match and even exceed mass and size of chicks exposed to warm conditions by the age of 3 weeks. The initial delay in growth rate resulted in a mild reduction in size of cold-exposed quail-chicks relative to chicks in warm conditions, but at one to two weeks of age growth rate of the two groups was similar, and in older chicks the increase in mass of cold-exposed chicks even exceeded that of chicks raised in warm conditions.

Interpretation – These results suggest that in conditions where ambient temperature limits the development of chicks, maturation of function is favoured at the cost of growth. This shift in balance became visible when environmental conditions were limiting. The limitation is evident from the fact that, initially, cold-exposed chicks spent less time foraging than required to sustain growth, while during that brief amount of time their body temperatures dropped significantly. This is in contrast to foraging shorebird chicks on the tundra at Churchill, where ambient conditions were not limiting, leaving the chicks ample leeway for development of both growth and mature function. To finish with the issue of developmental plasticity, both the quail chicks constrained by the cold environmental conditions and the shorebird chicks living under not so limiting conditions, have considerable latitude to modify the relationship between growth rate and mature function.

Limits to low body temperature in precocial chicks – chapter 8

Background – Body temperature is very flexible in young chicks of precocial species. Homeothermy develops rapidly compared to altricial species, but during the first days after hatching, body temperature decreases when the chicks are exposed to cold. This means that during foraging, body temperature falls when ambient temperatures are low. The physiology of the chicks is such that they can continue foraging as body temperatures fall, and chicks can survive body temperatures as low as 26°C (Myhre & Steen 1979). However, as body temperature drops, the machinery of the chicks is increasingly affected (chapter 7). Movements become sluggish at some point and increasingly so until movement eventually is inhibited completely and the chick lies immobilized. The ability to call is one of the last functions that remain unaffected by the cold, and allows the chick to be located and rewarmed by the adult, and recover.

The minimum body temperature that a chick will allow during foraging strongly affects the amount of time it has for foraging, and therefore is an important aspect in precocial life. Especially in environments where time is limited, e.g. through cold ambient temperatures such as in the arctic regions, regulation of body temperature is crucial to the survival of the precocial chick. Very few studies report body temperatures of precocial chicks during foraging (but see Myhre & Steen 1979, Joest 2003).

Question & approach – We found that chicks of free-living golden plovers and chicks of quail experimentally exposed to low ambient temperatures did not reduce their body temperature below ca. 36°C (chapters 6&7). This suggests that below this temperature the disadvantages related to physiological processed outweighed the advantages of continued foraging. To investigate this apparent limit in further detail, we investigated body temperatures of various species of precocial shorebird chicks foraging under semi-natural conditions in outdoor enclosures under varying ambient conditions. Body temperatures were measured with temperature-sensitive transmitters implanted in the body cavity, or by taking temperatures rectally.

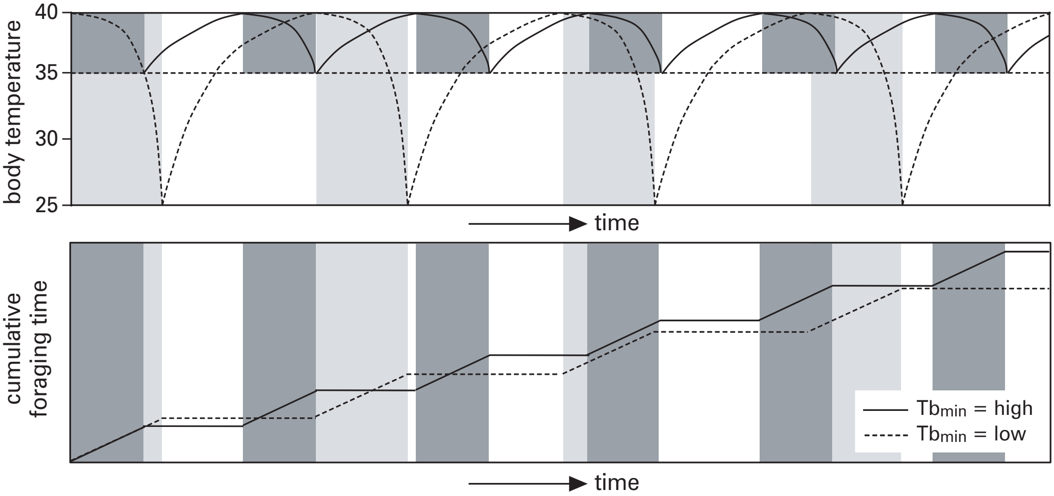

Figure 1.9. Hypothetical diagram of the duration of foraging and brooding bouts when chicks maintain different minimum body temperatures, illustrating that overall foraging time increases when chicks maintain T_b at higher levels. Upper panel: T_b as function of time, of chicks foraging until T_b=35°C or 25°C at mimimum (continuous resp. dashed line). Foraging bouts shown in grey (light grey: minimum T_b 25°C; dark grey: minimum T_b 35°C). T_b decreases increasingly fast during foraging, and increases during passive rewarming while chicks are being brooded by the parent. Lower panel: cumulative foraging time under both conditions (same as fig. 8.7).

Results – Chicks of whimbrel, Hudsonian godwit, lesser yellowlegs, dunlin and least sandpiper all ended foraging bouts and returned to their artificial brooder before body temperatures fell below 35°C. Modelling the rate of heat loss showed that a further reduction of body temperature did not increase the available foraging time, but rather reduced it, due to an increase in brooding time that is needed to regain body heat.

Interpretation – Tolerating reduced body temperature has certain advantages for a foraging precocial chick, such as higher survival chances in case brooding is delayed for some reason, and also a reduction of the rate of heat loss to the environment, because the thermal gradient between chick and environment is reduced. However, lowering their body temperature also has significant disadvantages, including reduced growth rate (Krijgsveld *et al.* 2001 (chapter 4), Gillooly *et al.* 2002, Kristan & Hammond 2002), reduced muscle performance and locomotor ability (likely affecting prey capture rate) (Norton 1973, Aulie 1976, Bennett 1990, Choi & Bakken 1991, own observations), and reduced rate and efficiency of digestion (Kleiber & Dougherty 1934, Osbaldiston 1966, see also chapter 7). In addition, energy expenditure during foraging is high (Schekkerman & Visser 2001, Krijgsveld *et al.* 2012 [ch. 5]), and the metabolic rate of a chick initially increases in order to maintain high body temperatures (Ricklefs & Williams 2003). Furthermore, the overall amount of time spent foraging will not increase when body temperature decreases further. This is because body temperature drops increasingly fast when the chick continues foraging (Krijgsveld *et al.* 2003a,b [chapters 6 & 7]), and therefore little foraging time is gained with each degree of body temperature lost. Moreover, the subsequent passive rewarming means that the time needed for the chick to rewarm will be increasingly long when body temperature is lower (fig. 1.9).

Because of these considerations, low body temperatures are not profitable for growing and self-foraging precocial chicks. They can survive body temperatures well below 30°C, and this benefits survival chances when chicks involuntarily have to endure extended periods of cooling, but they do not benefit growth. Instead, by reducing foraging bout length and increasing brooding time and thus maintaining a high body temperature, chicks can considerably reduce energy expenditure, while simultaneously increasing rate and efficiency of digestion.

Synthesis

This thesis is about the development of precocial chicks of shorebirds in relation to demands set by the arctic environment. In particular, it is about the effects that body size has on growth and development of functional maturity, and on the role of behavioural adaptations in response to environmental and physiological limits to maximize growth (fig. 1.10).

I have shown that precocial chicks of shorebirds maximize survival by combining a high growth rate with high levels of functional capacity, and are deploying a high flexibility in development and foraging behaviour to adjust to demands set by varying ambient conditions.

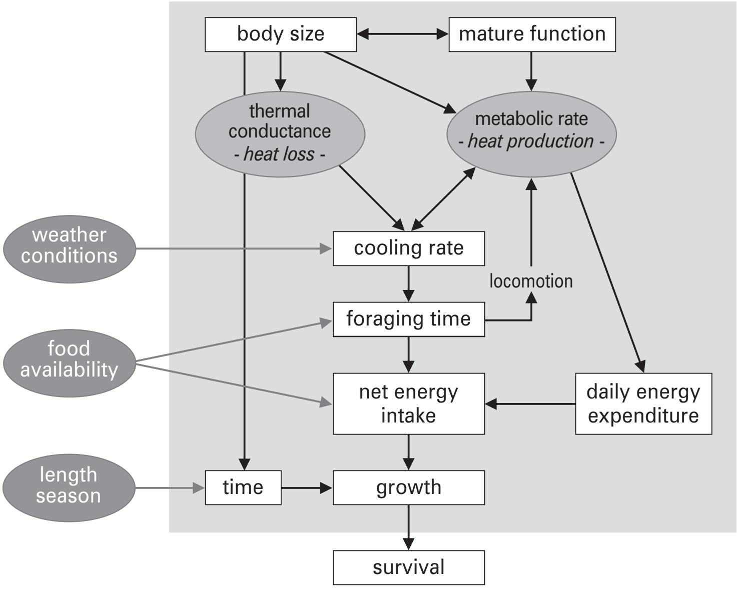

Figure 1.10. Schematic diagram showing the main aspects affecting growth and ultimately survival that were studied in this thesis. Chicks of larger species rely on their body size to limit heat loss resulting in lower mass-specific metabolism, but simultaneously they need more time to complete growth. Chicks of smaller species rely more on functional capacity of muscle tissue to generate heat and prevent cooling, at the cost of high mass-specific energy expenditure, while at the same time they grow fast. Environmental conditions such as weather, food availability and length of the season form external constraints limiting growth, and the chicks respond to this by adjusting their behaviour.

The main findings are:

1. Chicks of small species combine a high level of mature function (*i.e.* catabolic capacity and daily energy expenditure) with high growth rates, while larger species limit functional capacity in favour of growth.

   These results imply that whereas chicks of small species rely more on the functional capacity of their muscles to generate heat, chicks of large species with their larger mass can rely much more on heat retention to maintain their body temperature instead of increased function. A high level of functional maturity seems to be less important in larger chicks, and consequentially they may reduce their daily energy demand by lowering their level of functional maturity.

2. Low ambient temperatures can result in a shift in the balance between growth rate and mature function, in favour of mature function.

3. Mature function however is not necessarily challenged by low ambient temperatures, because chicks reduce foraging bout lengths in response to low ambient temperatures in order to limit heat loss and daily energy expenditure.

   These three results suggest that at least chicks of precocial species have considerable latitude to modify the relationship between growth rate and mature function. Although there is ample evidence for a trade-off between investment in growth versus mature function, both from the literature and from this study, conditions at Churchill were possibly too mild to elicit this trade-off, and rather illustrated the high level of physiological and behavioural flexibility of the chicks.

4. Growth is maximized by maintaining minimum body temperature at relatively high levels of 36-37°C.

   In doing so, the chicks avoid increase in energy expenditure and decrease in motor function that are related to a further decrease in body temperature, as well as a disproportionate increase in brooding time needed to passively regain body heat. As a result, the chicks have more time available for foraging than when they would extend foraging bouts at the cost of body temperature, and thus maximize growth. The physical ability of young precocial chicks to lower their body temperature to values as low as 26°C is not profitable for growth. The advantage of this phenomenon, which is so typical for shorebird chicks, lies in the fact that it enables them to survive periods of extended cooling, which is extremely useful in the arctic environment.

Part 1

Setting: chick growth rates and food availability


Photo: Gabe McNett

Chapter 2

Growth rates of seven species of arctic shorebird chicks varying in size

Karen L Krijgsveld & Robert E Ricklefs

Abstract

We measured growth rates of seven species of hand-raised shorebird chicks ranging in size from 4 to 33 g neonatal body mass. Species were least sandpiper *Calidris minutilla*, dunlin *C. alpina*, lesser yellowlegs *Tringa flavipes*, short-billed dowitcher *Limnodromus griseus*, American golden plover *Pluvialis dominica*, Hudsonian godwit *Limosa haemastica* and whimbrel *Numenius phaeopus*. Hatch dates and growth periods coincided with the period of peak food abundance on the tundra. Growth patterns reflected differences in neonatal as well as asymptotic size measurements, such as bill and tarsus length.

As expected, growth rates of body mass, and wing, tarsus and culmen lengths were higher in the smaller species: least sandpiper and dunlin. The intermediate-sized American golden plover and short-billed dowitcher showed comparatively slow increase in body mass for their size. The larger species needed yet more time to complete growth.

At hatching, the larger species had the lowest body mass relative to adult mass, and this difference narrowed slowly over the course of development. In contrast, the relative size of the tarsus was higher at hatching in the larger species than in the smaller species, and relative wing length showed a rapid increase. Species of intermediate size hatched at a high proportion of adult body mass, but the difference relative to the other species decreased rapidly during development. The smaller species hatched at a higher proportion of adult size than the largest species, and achieved adult size most rapidly.

The large among-species variation in growth pattern may help us to understand observations on related aspects of development, such as catabolic capacity, energy expenditure, and time energy budgets.

Introduction

The rate of growth of young individuals is an important life-history parameter affecting survival during juvenile development and fitness components much later in life. In many species, the rate of growth is largely determined by the level of investment by the parents: the more they feed their offspring, the faster their growth and the higher their fitness prospects. In precocial shorebird chicks, however, parental investment is confined to brood guarding, post-hatching brooding and habitat selection. Feeding is left to the chicks themselves, although parents lead the chicks to suitable habitat (Oken 1837, Nice 1962). Just hours after hatching, chicks leave the nest and start foraging. Because of this, their growth rate is largely determined by their own behaviour and physiological capabilities. This is in sharp contrast to chicks of altricial species, which are fed by their parents and thus are more dependent on them for their growth and survival.

Growth rate of precocial shorebird chicks thus is not only determined by their food intake, but also by their mobility and capacity for thermoregulation, because these affect the chick's ability to collect food. This dependence on functional capacity affects growth patterns and poses a potential conflict between increase in size and increase in mature function (Dawson & Evans 1957, Ricklefs 1979). Locomotory and thermoregulatory capacities of young birds depend on the level of functional maturity of the skeletal muscles (Choi *et al.* 1993, Olson 1994, Marjoniemi & Hohtola 1999). This maturity is achieved through the development of the contractile and metabolic machinery within muscle fibers, rather than the proliferation of these muscle fibers as is needed for increase in size (Hohtola & Visser 1998). Growth in precocial shorebird chicks therefore requires relatively high levels of functional maturity, compared to chicks of altricial birds (Ricklefs 1973). This higher degree of functional maturity results in a reduced growth rate, because in general, mass-specific growth rate decreases with increasing development of functional capacity (precocity) of the neonate (Ricklefs 1968, Starck & Ricklefs 1998). As a consequence, precocial chicks need more time to complete growth than altricial chicks (Ricklefs 1973, Starck & Ricklefs 1998). Time is, however, limited for shorebird species that breed in arctic regions, and increasingly so at more northerly latitudes. The breeding season is defined by a brief period of elevated ambient temperatures and food abundance (see chapter 3). The length of the season thus defines the maximum time available to chicks to complete the developmental stage.

In this respect, body size is an important factor. Chicks of larger species need more time to complete growth than chicks of smaller species (Ricklefs 1968). For them, the shortness of the arctic breeding season would favour high growth rates in arctic zones. Simultaneously, the cold climate in arctic environments imposes an additional need for mature function not only for locomotory activity, but also to meet the high energy demand for thermoregulation. Growth also results in a more favourable surface-to-volume ratio and thus a decrease in the relative rate of heat loss, which is especially important for smaller species because they have a less favourable surface-to-volume-ratio. In smaller species, therefore, arctic conditions would favour both rapid growth and high levels of mature function. Accordingly, larger and smaller species might adopt different strategies to resolve the trade-off between growth and tissue maturation.

Chicks of precocial species breeding in the arctic have relatively high growth rates compared to their more temperate conspecifics (Ricklefs 1973, Beintema & Visser 1989a, Schekkerman *et al.* 1998, 2003, Tjorve *et al.* 2009). Simultaneously their level of functional maturity is high, as inferred from high levels of catabolic capacity (Krijgsveld *et al.* 2001; chapter 4), daily energy expenditure (Krijgsveld *et al.* 2012; chapter 5) and metabolic response to cold (Ricklefs & Williams 2003). These results suggest that birds have considerable latitude to modify the relationship between growth and mature function.

To compare growth strategies between smaller and larger species, we measured growth rates from hatching onward of laboratory-raised chicks of six species in the family Scolopacidae: least sandpiper *Calidris minutilla*, dunlin *C. alpina* (both subfamily Calidridinae), lesser yellowlegs *Tringa flavipes*, Hudsonian godwit *Limosa haemastica*, whimbrel *Numenius phaeopus* (all three subfamily Tringinae), and short-billed dowitcher *Limnodromus griseus* (subfamily Gallinagininae), as well as the American golden plover *Pluvialis dominica*, a member of the Charadriidae. These species cover a large range in body size, from 4 grams in least sandpiper neonates to 33 gram in whimbrel neonates, representing an 8-fold difference. We relate growth rates, hatching dates and time needed to complete growth to the demands imposed by the arctic environment to provide insight into the developmental adaptations to growing up under arctic environments.

Methods

Birds and housing

Eggs were collected on the tundra near Churchill, MB, Canada, in June 1995–1998. Eggs were incubated at 36.5–37.5°C, at a relative humidity of 55% until shells were starred (2–3 days before hatching), when relative humidity was increased to 85%. Hatching success was 80–90%, including eggs where there was no development at all and which may therefore have been infertile. For all species, the mean hatching date fell within a few days of July 1st (table 2.1). The day of hatching was designated as chick age 0.

Chicks were kept in small groups of 4 to 6 chicks in cardboard boxes (ca. 1 m × 0.5 m) fitted with light bulbs to provide warmth. This created a range in air temperatures between 25 and 38°C, in which the chicks could select their preferred thermal environment. At later ages, when the chicks had become homeothermic, the light bulbs were removed and the chicks were kept at ambient room temperature. Chicks stood on a 0.5 cm^2 mesh-wire cloth floor elevated above a layer of sawdust placed on the floor of the box for hygiene and easy cleaning. All chicks were provided *ad lib* with water and food. Food consisted of pheasant starter type II-mix (Spelderholt, Beekbergen, Netherlands) or a similar turkey pre-starter mix (Puratone Corporation, Niverville, Canada), supplemented with a mix of canned tuna, boiled chicken, boiled and fresh eggs and oatmeal, as well as freshly-caught and frozen mosquitoes. Nutrients of the food were proportioned to resemble natural insect food.

From one day after hatching, chicks were moved to an outside enclosure for periods of a few hours up to a few days or, for golden plovers, longer. The enclosure was circular with a diameter of ca. 10 m, and surrounded by a chicken-wire fence 50 cm high, lined along the lower 20 cm with cloth and plastic, and fixed firmly to the ground with tent pegs to prevent escapes. A cover of large mesh netting kept out predators. An artificial brooder provided heat to the chicks. It consisted of a wooden box of 20 (height) × 30 (depth) × 20 (width) cm, with an entrance of 15 × 15 cm, in which a light bulb and a thermal blanket were placed, maintaining a temperature of up to 41°C closest to the light bulb. The light from the bulb served to direct the chicks to the brooder. Chicks learned to enter the brooder to be rewarmed within two days. From that day onward they were left in the enclosure for longer periods of time, varying between several hours up to several days, depending on weather conditions (young chicks) and observation protocols for related experiments (see chapters 5 & 6). Because chicks rapidly consumed naturally available food in the enclosure, food and water were supplied daily. Food was scattered on the ground to simulate natural foraging conditions.

Egg collecting was carried out under permit from the Canadian Wildlife Service and husbandry and laboratory procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri-St. Louis.

Measurements

Chicks were weighed and measured in the morning, generally around 9:00 h. Body mass was measured daily during the first two weeks after hatching, to monitor and ensure proper development of the chicks. After this time, chicks were weighed every other day or every 3 days. We measured external appendages (length of tarsus, wing [maximum length of chord], and culmen [tip of bill to nasal feathers]) either daily or once every three to five days, depending on the year.

Growth curves and statistical analysis

Unless mentioned otherwise, data were analyzed with general linear models (GLM) using SPSS version 12 (SPSS Inc. 2003) and Genstat version 13.

Estimates of growth parameters were obtained by nonlinear curve fitting of the logistic growth equation: mass or size = $A/(1+\exp(-K\times(\text{age}-t_i)))$, where A is the asymptote (g or mm), K is the growth rate constant (d^{-1}) and t_i is the inflection point of the growth curve (d). Growth parameters were fitted using SPSS version 12 (SPSS Inc. 2003). For most of the species, the logistic growth function fit growth data better than the Gompertz function (higher r^2: own data, Schekkerman *et al.* 1998), and therefore only logistic curves are shown in this chapter. For comparison with other studies, the logistic growth rate parameter K can be converted approximately to the Gompertz K by the expression $K_G = 0.68K_L$ when assuming identical asymptotes (Ricklefs 1973).

Because we stopped measuring chicks before they reached asymptotic size, and because we did not handle adult birds, values of A were estimated from published values for adult measurements. Only A for tarsus length was estimated by curve fitting, as the tarsus of an adult is shorter than its maximum length in a chick, and would thus result in underestimating tarsus growth rate. We used published adult measurements obtained from breeding birds in Canada and in Alaska, except for dunlin for which we used sizes measured in southern Scandinavia, and short-billed dowitcher, for which we used sizes measured during fall migration (Jehl 1963, Jehl & Smith 1970, Johnsgard 1981, Skeel 1982, Hayman *et al.* 1991).

Results & discussion

Hatching dates
The incubated eggs hatched highly synchronously within years, primarily during the first week of July, with the overall mean for all eggs on July 3 (table 2.1, fig. 2.1). Hatching dates of artificially incubated eggs corresponded closely with those of natural nests (own observations, pers. comm. J. Jehl Jr., Jehl 2004). Over the four years of study, annual mean hatching dates varied 7 days on average, with the largest variation in the short-billed dowitcher (15 days) and the smallest variation in the lesser yellowlegs (3 days). Short-billed dowitchers were the first to hatch (first neonate June 24, mean hatch date June 30), but were also among the last chicks to hatch (last neonate July 14). Only Hudsonian godwit and whimbrel chicks hatched later than dowitchers (last neonate July16 in both species). Average and range of hatching dates of these chicks of the larger two species fell a few days later than that of the smaller species. Golden plovers also hatched comparatively late, and these chicks had a relatively narrow range of hatching dates. Differences in hatching dates between free-living and hand-raised golden plover chicks can be attributed to the fact that data on free-living golden plover chicks were mostly from 1994, while data on hand-raised chicks were all from 1995-1998. The last chicks hatching in the field were found as late as July 19 (July 11 in the lab).

Size at hatching
Neonatal body mass of the chicks varied between 4 and 33 grams (table 2.2). The rate of growth in mass of the chicks increased among species in the following order: least sandpiper, dunlin, lesser yellowlegs, short-billed dowitcher,

Table 2.1. Mean, minimum and maximum hatch date of seven species of hand-raised shorebird chicks, between 1995 and 1998, and of free-living American golden plover chicks in 1997 and 1998. N is the number of hatchlings.

species	hatching date			n
	min	mean	max	
least sandpiper	28 Jun	2 Jul	6 Jul	26
dunlin	27 Jun	3 Jul	13 Jul	45
lesser yellowlegs	26 Jun	2 Jul	8 Jul	21
short-billed dowitcher	24 Jun	30 Jun	14 Jul	21
Am. golden plover (lab)	1 Jul	5 Jul	11 Jul	24
Am. golden plover (field)	2 Jul	7 Jul	19 Jul	32
Hudsonian godwit	27 Jun	6 Jul	16 Jul	25
whimbrel	30 Jun	5 Jul	16 Jul	53
overall	24 Jun	3 Jul	19 Jul	247

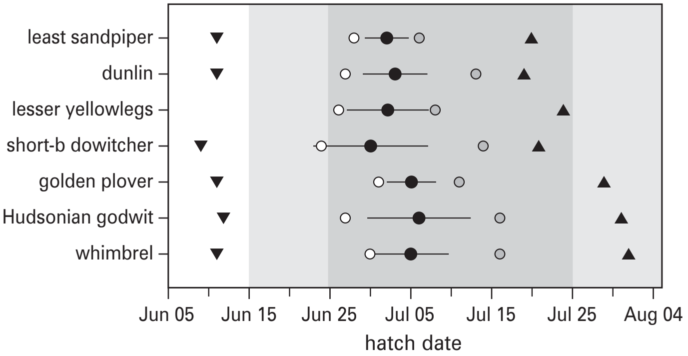

Figure 2.1. Hatching dates of laboratory-raised chicks (mean = black circle; sd = horizontal line; minimum and maximum = white and grey circles). Also shown are average laying date and average date at which sustained flight is achieved (triangles; based on incubation period and age of sustained flight; Cooper 1994, Cramp 1998, Elphick & Klima 2002, Jehl 2004; sustained flight for lesser yellowlegs, short-billed dowitcher and golden plover estimated from own observations, based on feather development and behaviour). Shaded areas indicate the period of food availability (general period = light grey, peak abundance = dark grey, from chapter3).

Table 2.2. Neonatal (0 days) sizes of seven species of hand-raised shorebird chicks, and free-living American golden plover chicks. Mean values are shown along with standard deviation (sd) and the number of chicks that were measured (n).

species	mean	sd	n	mean	sd	n
		body mass			**wing**	
least sandpiper	4.2	0.46	14	9.4	1.27	13
dunlin	7.8	0.62	30	12.8	1.10	21
lesser yellowlegs	11.4	0.49	6	14.8	1.94	6
short-billed dowitcher	12.3	0.91	15	14.0	1.12	14
Am. golden plover (lab)	17.8	1.93	5	18.3	1.15	3
Am. golden plover (field)	19.5	1.30	23	19.2	0.84	5
Hudsonian godwit	24.9	2.37	11	17.9	1.61	10
whimbrel	33.4	2.49	23	20.3	1.87	18
		tarsus			**culmen**	
least sandpiper	16.7	1.28	14	7.4	0.61	13
dunlin	23.0	1.30	24	11.3	2.04	24
lesser yellowlegs	29.4	1.32	6	12.7	1.46	6
short-billed dowitcher	26.7	1.13	14	15.4	0.72	14
Am. golden plover lab	34.3	3.13	3	11.9	0.91	3
Am. golden plover (field)	31.9	2.46	16	11.4	0.74	16
Hudsonian godwit	33.0	6.29	10	16.1	1.03	10
whimbrel	34.2	1.64	20	17.1	0.87	19

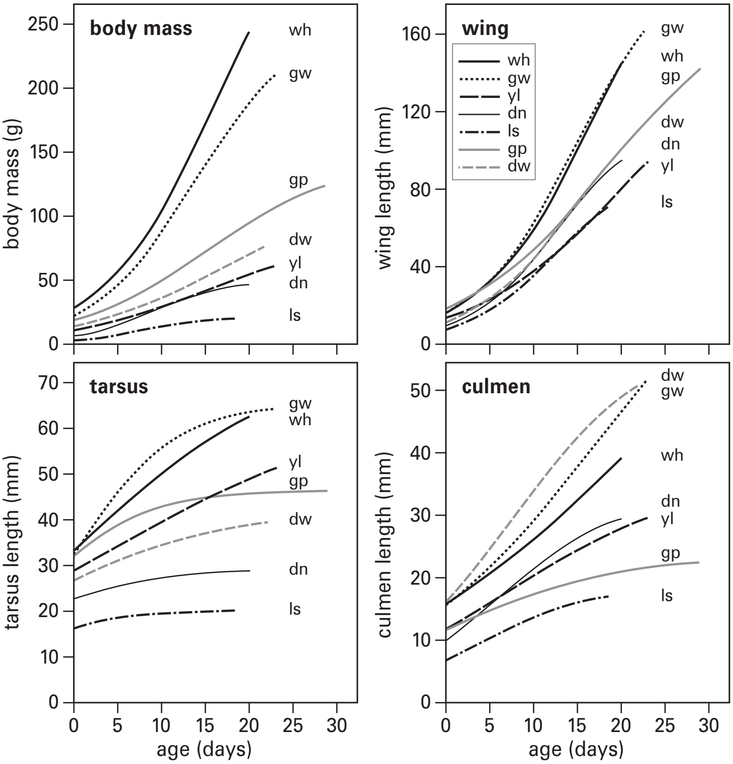

Figure 2.2. Growth patterns of seven species of charadriiform chicks of varying sizes, shown for body mass, wing, tarsus and culmen. Species are, from large to small: whimbrel (wh), Hudsonian godwit (gw), American golden plover (gp), short-billed dowitcher (dw), lesser yellowlegs (yl), dunlin (dn), and least sandpiper (ls). Indicated with grey lines are golden plover and dowitcher. All belong to the family of Scolopacidae, except golden plover which belongs to the family of Charadriidae.

American golden plover, Hudsonian godwit, whimbrel. The growth rates of external appendages showed a similar order, except that wing and tarsus were shorter in dowitchers than in yellowlegs, contrary to body mass (table 2.2). In addition, the charadriid plovers had much shorter bills for their body size than their scolopacid sandpiper relatives; not much longer than those of the much smaller dunlin.

Free-living golden plover chicks were somewhat heavier and had larger wings at hatching than chicks that hatched in the incubator, but this difference was due to variation between years and possibly also observers. This is shown by the fact that free-living neonates were slightly heavier in 1994, when most field-measurements were obtained, than in later years (avg = 19.9 g for 11 neonates in 1994 vs 18.6 g [n = 8] in 1997 and 19.4 g [n = 12] in 1998). In 1997, there was no difference between free-living chicks and chicks hatched in the lab (avg = 18.9 g for 7 chicks), except for the wing which was 2 mm longer in free-living neonates.

One day after hatching, mean body mass was lower than on the day of hatching in all species, as chicks used yolk reserves prior to learning to feed. Two days after hatching, body mass was without exception higher than at the day of hatching. Sizes of wing, tarsus and culmen showed an increase from the day of hatching onward.

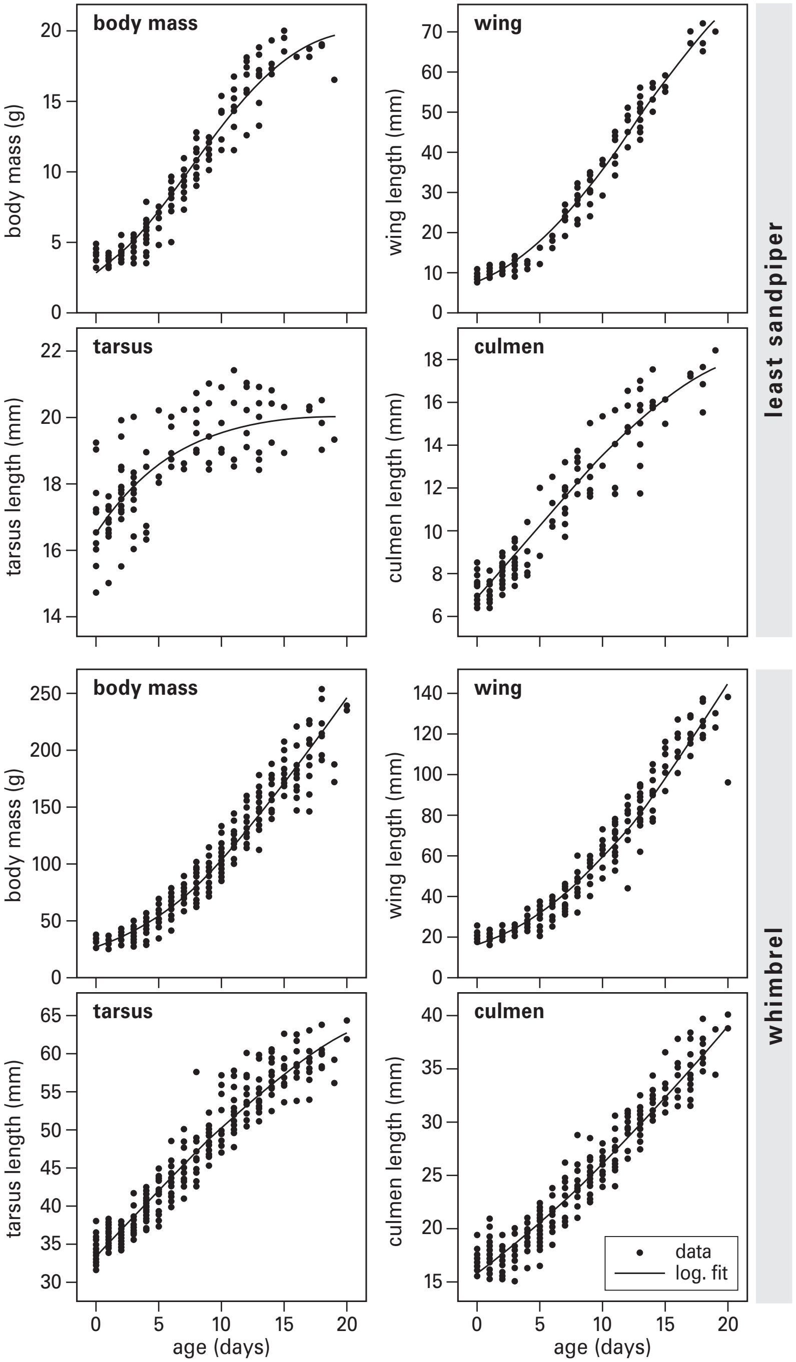

Figure 2.3. Individual measurements of body mass and external sizes of chicks of least sandpiper and whimbrel across the first three weeks of age, showing variation in mass and size. Logistic growth function is plotted as well, to show the fit to the data. Note the difference in scale on the Y-axes.

Absolute size

The whimbrel, being the largest species, had the highest body mass throughout the growth period (fig. 2.2). Most of the other species increased in mass in the same order of size as at hatching. Exceptions to this pattern were the development of dunlin and lesser yellowlegs. Although lesser yellowlegs were heavier both at hatching and at the end of the growth period, they grew much more slowly than dunlin, so that between ca. 7 and 14 days of age, body mass of the two species was similar.

Structural sizes deviated from this pattern in several ways. Wings of whimbrel were similar in length to those of the Hudsonian godwit, the tarsus started out at similar length but eventually grew to a larger size, whereas the culmen also started out at similar length, but grew to a smaller asymptotic size compared to the Hudsonian godwit. The culmen of short-billed dowitcher chicks rapidly exceeded those of Hudsonian godwit and whimbrel in length, and remained the longest throughout the first three weeks of development. Beyond that age, the more slowly growing culmen of the Hudsonian godwits exceeded that of the dowitchers.

Individual growth data of least sandpiper chicks and of whimbrel chicks show the amount of variation in size for chicks of similar ages (fig. 2.3). The logistic growth functions are plotted in these graphs as well, showing that at young ages even the logistic function, which matches the data of especially young chicks better than the Gompertz' growth function, does not fully describe the data, especially with regard to body mass and wing length. These growth patterns, with the initial delay in increase, are typical for precocial shorebird chicks.

Growth rate

As expected, growth rates varied with body size: the smaller the asymptotic size, the higher the growth rate (values of K and t_i in table 2.3). Chicks of the larger whimbrel had lower growth rates than chicks of the smaller Hudsonian godwit for mass, wing and tarsus, and also for the culmen, which grew to a smaller size than that of the Hudsonian godwit. The chicks of the other scolopacid species – least sandpiper, dunlin and short-billed dowitcher – likewise exhibited growth rates that were consistent with their size. Chicks of the lesser yellowlegs however grew slowly for their size, with respect to both body mass and the external appendages. Chicks of the American golden plover exhibited relatively slow growth of body mass and wing, but a rapid growth of the tarsus. Short-billed dowitchers grew slowly with respect to body mass, but rapidly with respect to wing, tarsus and culmen.

Analysis of the growth parameters showed that growth rate was indeed negatively correlated with asymptotic size (fig. 2.4). Because only few species were included in this analysis, the relationship of growth parameters to asymptotic size was significant for the inflection point, but only a trend for the growth rate constant. This was tested using an accumulated GLM, in which the effect of the type of measurement (*i.e.* mass, wing, tarsus, bill) was accounted for prior to testing the effect of the asymptotic value on either K or t_i. Thus, the relation between A and K or t_i could be tested in a single model for all types of measurements combined (accumulated GLM; effect of asymptotic size on t_i after correction for type of measurement: overall model: $F_{4,\,23} = 18.9$, $P < 0.001$, $r^2 = 0.73$; effect of asymptote: $t = 2.47$, df = 1, $P < 0.05$. Effect of asymptotic size on growth constant K: $t = -1.8$, $P = 0.08$).

Regardless of the negative relationship between growth rate and body size, chicks of the larger species (whimbrel and godwit) showed a relatively high growth rate given their body size, compared to other shorebird species of similar size (fig. 2.5). Lesser yellowlegs, short-billed dowitcher and American golden plover on the other hand showed a relatively low growth rate given their body size, especially with respect to body mass.

Table 2.3. Growth parameters of seven species of shorebirds, raised under laboratory conditions in Churchill. Listed in order of increasing asymptotic body mass. Growth parameters were obtained by non-linear fitting of the logistic growth equation. A = asymptote (g or mm), K = growth constant, t_i = inflection point (d).

measure	species	A	K	t_i	r^2	n data	n chicks
mass	least sandpiper	21	0.240	7.7	0.952	179	26
	dunlin	50	0.225	8.9	0.940	355	44
	lesser yellowlegs	81	0.129	14.6	0.891	184	20
	short-billed dowitcher	113	0.124	16.1	0.918	207	21
	Am. golden plover lab	145	0.128	15.1	0.898	160	23
	Am. golden plover field	*145*	*0.164*	*11.3*	*0.930*	*68*	*49*
	Hudsonian godwit	255	0.170	13.9	0.918	263	25
	whimbrel	380	0.156	16.2	0.952	403	51
wing	least sandpiper	90.5	0.199	12.2	0.975	116	23
	dunlin	116.3	0.197	12.5	0.956	241	41
	lesser yellowlegs	154.5	0.122	19.4	0.824	102	20
	short-billed dowitcher	143.8	0.165	14.9	0.963	140	21
	Am. golden plover lab	179.5	0.121	18.1	0.822	82	24
	Am. golden plover field	*179.5*	*0.154*	*14.4*	*0.976*	*15*	*12*
	Hudsonian godwit	204.8	0.169	14.8	0.956	179	25
	whimbrel	243.5	0.152	17.4	0.957	258	45
tars	least sandpiper	20.2	0.192	-7.8	0.603	119	28
	dunlin	29.5	0.128	-9.4	0.665	244	43
	lesser yellowlegs	67.8	0.062	4.6	0.992	103	20
	short-billed dowitcher	42.8	0.089	-5.8	0.868	144	21
	Am. golden plover lab	46.4	0.170	-4.8	0.852	100	24
	Am. golden plover field	*44.7*	*0.132*	*-7.1*	*0.783*	*55*	*37*
	Hudsonian godwit	65.5	0.173	0.0	0.861	179	25
	whimbrel	74.7	0.093	2.3	0.931	284	49
culmen	least sandpiper	18.5	0.159	3.6	0.910	119	25
	dunlin	33.3	0.145	5.9	0.924	243	43
	lesser yellowlegs	35.5	0.101	7.1	0.919	103	20
	short-billed dowitcher	59.3	0.127	7.7	0.959	144	21
	Am. golden plover lab	23.5	0.107	0.3	0.893	99	24
	Am. golden plover field	*23.5*	*0.123*	*0.4*	*0.944*	*55*	*37*
	Hudsonian godwit	81.8	0.087	16.8	0.939	179	25
	whimbrel	80.0	0.068	20.6	0.944	282	49

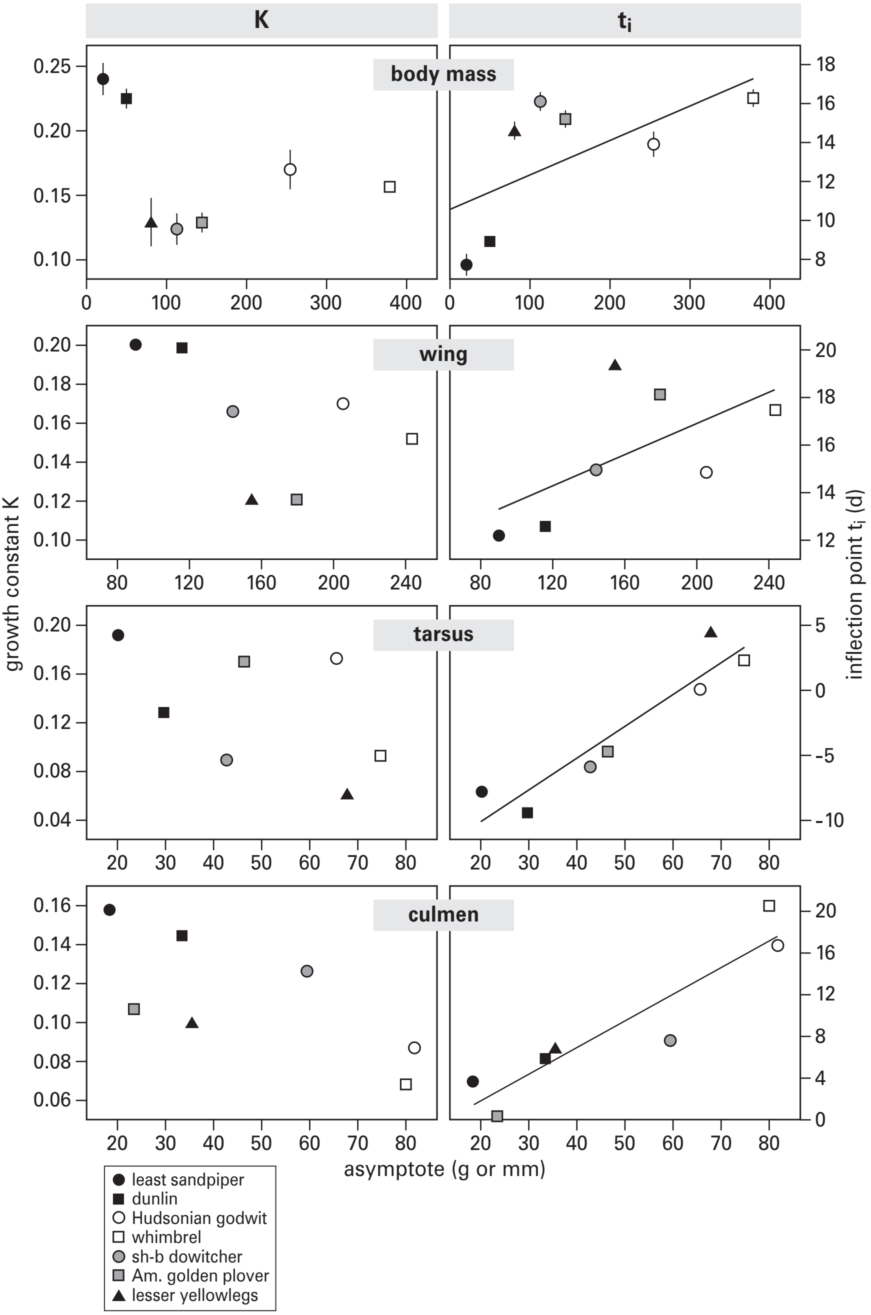

Figure 2.4. Relation between asymptotic size and growth rate, shown for all seven shorebird species, and expressed as growth constant K and inflection point t_i. Standard errors are shown for values of body mass. Asymptote fitted for tarsus; set for the rest of the measurements, based on adult sizes. Graphs show that chicks of smaller species have higher growth rates and complete growth at younger ages.

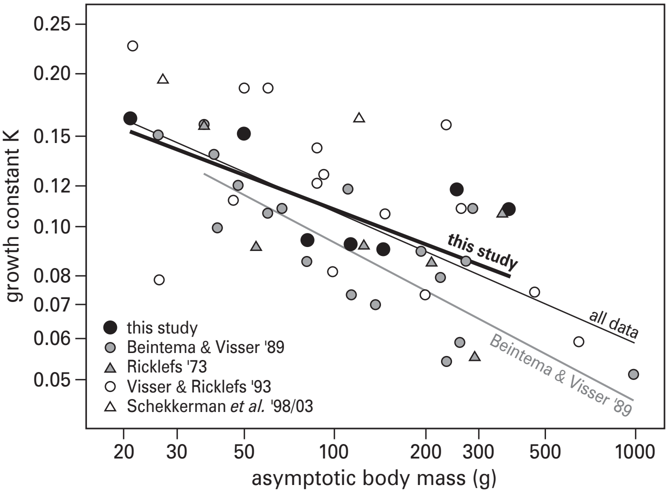

Figure 2.5. Data on growth rates in relation to body size of various species of shorebird chicks, as observed in this study in comparison with published data. Regression of all data combined: log K = –0.259*log A - 0.453.

Growth rate in comparison to other shorebird species

Neonatal masses of the chicks in this study closely matched data obtained at the same site in 1979 (Ricklefs 1984). The growth rates of chicks in this study fell within the range of growth rates published for precocial shorebird chicks (Ricklefs 1973, Beintema & Visser 1989a, Visser & Ricklefs 1993a, Schekkerman *et al.* 1998, Schekkerman *et al.* 2003) (fig. 2.5). Growth rate was higher in some of the hand-raised chicks of Visser & Ricklefs, and in chicks of little stint and red knot measured in the high arctic of Siberia by Schekkerman *et al.* (1998, 2003). Variation in latitude, raising conditions, and phylogeny may thus underlie differences in growth rates between species to a considerable extent. For example, growth rates were shown to increase with latitude by Klaassen & Drent (1991) and for shorebirds specifically by Tjørve *et al.* (2009).

Growth relative to adult size

When body mass and external sizes are expressed as proportion of adult mass or adult sizes, these values increase in a pattern that is inverse relative to rates of increase in the original measurements (fig. 2.6). Growth of least sandpiper, dunlin, godwit and whimbrel chicks more or less follow a common pattern, whereas the golden plovers, yellowlegs and dowitchers show some striking differences.

Smaller least sandpiper and dunlin hatched at a larger proportion of adult body mass than the larger godwit and whimbrel, and maintained these higher proportions during most of their development period. The same was true for wing length, apart from an initially even higher proportion of adult wing length in neonate golden plover chicks. Chicks of species of intermediate sizes (lesser yellowlegs, American golden plover and short-billed dowitcher) hatched at a relatively high percentage of adult body mass, but because of their comparatively slow growth (see also fig. 2.4), they showed lowest proportions of adult body mass attained by three weeks of age. A similar pattern is shown for wing length. In contrast, the largest species, the whimbrel and Hudsonian godwit, hatched at the lowest percentage of adult body mass relative to their conspecifics, but with a tarsus that was much closer to adult size than

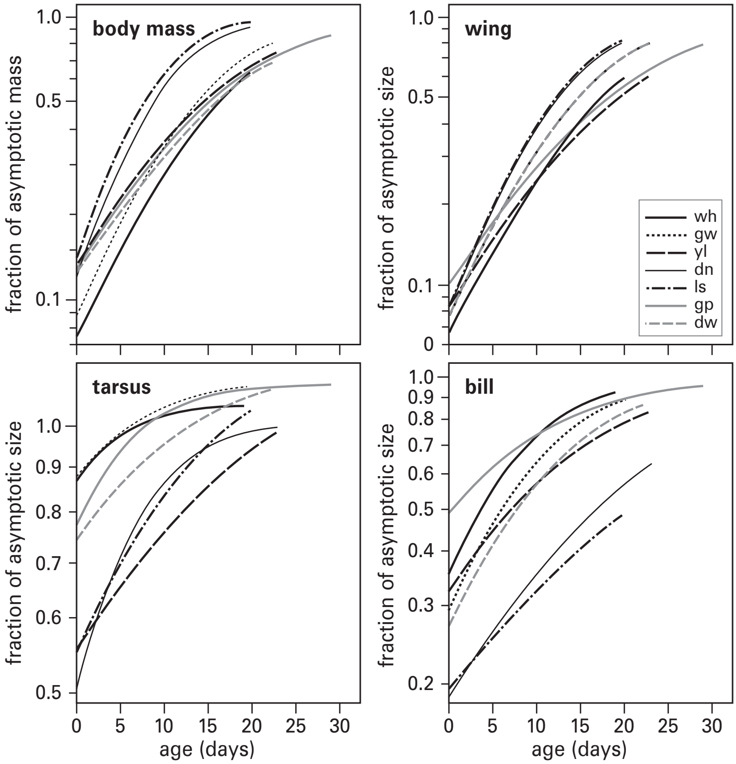

Figure 2.6. Relative mass and external sizes, shown as fraction of asymptotic mass or size that is attained at each age. Species are, from small to large: least sandpiper (ls), dunlin (dn), lesser yellowlegs (yl), short-billed dowitcher (dw), American golden plover (gp), Hudsonian godwit (gw), and whimbrel (wh). Smaller species started out at a higher proportion of adult mass and reached adult mass earlier, while tarsus and culmen of larger species started out at a higher proportion of adult size. Note the comparatively slow development of body mass in yellowlegs, golden plover and dowitcher.

those of the other species. After the first week of age the difference in proportional tarsus length decreased, and at this age the proportional wing length of whimbrel and Hudsonian godwit increased from lowest fraction of adult size to an intermediate fraction, in comparison with the other species.

Tarsus and bill of golden plover chicks had already reached a large proportion of adult size at hatching, and subsequently grew rapidly. This contrasted with their slow growth in body mass compared to the other species. The lesser yellowlegs, belonging to the same subfamily as the whimbrels and the godwits, started out at a higher proportion of adult mass and wing length, but at a much lower proportion of adult tarsus size, and their growth rate was considerably lower (see also fig. 2.4).

Because of their larger size and slower growth, chicks of larger species needed more time to complete growth than chicks of smaller species (fig. 2.3). This is true especially for growth of body mass. Chicks of least sandpiper and dunlin reached aymptotic size by two to three weeks of age, while the larger godwit and whimbrel chicks only reached asymptotic size at almost four weeks of age. External structures such as wing, tarsus and bill showed much more variation in time to complete growth, due to differences between species in final sizes, e.g. short versus long bills or legs (fig. 2.6).

In conclusion

Overall, growth rates were higher in smaller species, and larger species required more time to complete growth. In addition, smaller species hatched at a larger percentage of adult body mass than larger species. Regardless of this general pattern, growth patterns varied considerably among species, such as for instance growth rate of whimbrel and godwit chicks, which was relatively fast given their large body size. We hypothesize that these large species, that lose relatively little heat to their environment, invest relatively little in functional capacity and more in growth (see Krijgsveld *et al.* 2001 & 2012; chapters 4&5). Thus they may shorten the time needed to reach adult size, which is crucial for larger birds growing up in arctic areas with brief summer seasons. Previous research by Tjørve *et al.* (2009) has indeed shown that growth rates were higher in shorebird species growing in colder ambient conditions as well as in areas with shorter breeding seasons. These findings suggests that growth rates may be under selective pressure, and that physiological processes in the chicks, such as growth rate, metabolic rate and muscle function, may be adjusted to maximize chances of survival. The observed variation in growth patterns may thus not only reflect phylogenetic relationships of the species, but may also help us to understand observations on related aspects of development.

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Photo: Carel Windt

Chapter 3

Seasonal and diurnal patterns in arthropod abundance for shorebird chicks on the Canadian tundra at Churchill, Manitoba

Karen L Krijgsveld, Jan van Gils & Robert E Ricklefs

Abstract

We measured abundance of arthropod prey using sticky boards and pitfall traps on the tundra at Churchill, Manitoba, Canada, during three consecutive years, to relate foraging behaviour, energy expenditure and growth of shorebird chicks to food abundance. We collected insects from 38 families in 12 orders, the majority (78% of total number) being Diptera. Numbers trapped varied considerably between days, but increased between the end of June and the end of July. The maximum in mid July coincided with the time that shorebird chicks hatch and reach the age of sustained flight. At Churchill, the period of high food abundance was long enough for shorebird chicks to complete growth, even for chicks of slower-growing species such as golden plover, whimbrel and Hudsonian godwit. Compared to larger arthropod species, numbers of smaller species peaked earlier in the season, were elevated for a longer period of time, and were trapped in higher numbers. Thus, young chicks and chicks of small, fast-growing species could benefit from smaller prey early in the season, while larger and more slow-growing species could benefit from larger prey as they grew larger toward the end of the season. Arthropod abundance was highest during daytime, between late morning and early evening. This diurnal pattern was caused mainly by Diptera, which have previously been shown to constitute the main prey of shorebird chicks. Foraging bouts of golden plover chicks were longer when food abundance was higher. This was possibly related to lower wind speeds and lower but increasing ambient temperatures during that time of day, which has previously been shown to relate to higher prey capture rates of shorebird chicks.

Introduction

In arctic regions, shorebird chicks face two major problems (e.g., Chernov 1985, Carey 1986). One is the brevity of the arctic growing season. This forces chicks to complete their development quickly. Slowed growth can result in poor condition at the start of their southward migration. The second problem is the cold arctic climate. Cold exposure leads to increased energy expenditure, which may exceed energy intake. Cold exposure also might require earlier maturation of muscle tissue to produce sufficient heat at lower temperatures to maintain body temperature, which in turn could reduce the growth rate of muscle (Ricklefs 1994, Starck & Ricklefs 1994, Choi & Ricklefs 1997, Starck & Ricklefs 1998). The relevance of food availability lies in the fact that it affects both the time that the chicks must spend foraging and their exposure to cold temperatures. On top of that, food availability itself is also strongly related to seasonal variation in climate and prevailing weather conditions, with higher arthropod activity when ambient temperatures are higher, as was shown in the extensive studies carried out at Barrow, Alaska, in the 1960s (Holmes 1966, Holmes & Pitelka 1968, MacLean & Pitelka 1971) and in the review by Danks (1999).

For chicks of different sizes, different aspects of food availability are important. For chicks of larger species, which have longer development periods (Ricklefs 1973), the length of the period with sufficient food availability in the summer season is crucial. For chicks of smaller species, which lose body heat rapidly, the quantity of food is particularly important, especially during cold conditions. The variability in quality and quantity of food is therefore an important factor for both smaller and larger species. To understand growth patterns and foraging behaviour of the chicks, we therefore need to know how food availability varies through the season and with weather conditions.

The foods of shorebirds cover a wide variety of invertebrate taxa (Holmes 1966, Baker 1979, Skagen & Oman 1996). The main prey of chicks consists of a wide variety of arthropods (Holmes

1966, Holmes & Pitelka 1968) that are captured from the soil and the sparse, low vegetation. We studied the availability of these arthropod prey items on the tundra at Churchill, Manitoba, during three consecutive years, to relate foraging behaviour, energy expenditure and growth of shorebird chicks of different sizes to their environment. We measured food availability over the course of the breeding season, changes in food availability in relation to environmental conditions such as wind and ambient temperature, and changes related to the time of day.

Material & Methods

Sampling

We measured the availability of arthropods during the breeding season between June 6 and August 4, from 1995 through 1998, on the subarctic tundra near Churchill, Manitoba, Canada (58° 84' 59" N, 94° 80' 49" W). In midsummer, the sun rises there at 03:20 h and sets at 22:00 h, with a long period of civil twilight, from 01:45 h and until 23:30 h.

Flying insects just above the vegetation were trapped using sticky boards. These were flexible, yellow plastic sheets measuring 25×10 cm that were covered with a sticky resin (brand Horiver, Kringkoop, Blijswijk, Netherlands). Arthropods that touched the boards were trapped in the resin and remained there until the boards were removed from the tundra. The sticky boards were wrapped around empty beer bottles, using two paperclips to keep them in place, and these traps were then placed on the soil between the vegetation, the bottles upside down with the neck in the ground. Twelve sticky boards were set out in two lines of six traps placed ca. 2 m apart. One line was set out in dry habitat with vegetation of lichens and small willows; the other line was set out close to (ca. 20 m) the first line in wet habitat with vegetation of lichens and sedges.

Ground-dwelling insects and spiders, as well as limited numbers of other invertebrates such as snails, were trapped using pitfall traps. Pitfalls consisted of white plastic cans with a diameter of 10 cm and a depth of ca. 15 cm. They were filled with ca. 3 cm of a solution of 10% formalin, to which a drop of dishwashing liquid was added to reduce surface tension. Twelve pitfalls were placed in the field similarly to the sticky boards and in the same area.

To measure seasonal patterns of food availability and the effect of weather conditions and season on food availability, we took samples either every day (1995) or every four days (1996, 1997, 1998), throughout the season. Sticky boards and pitfalls were usually set out in the evening. Arthropods were collected after 24 hours, unless variation throughout the day was measured (see below). For this purpose, sticky boards were taken down with insects on them, and wrapped in cellophane. Contents of pitfalls were drained and collected in plastic bags. All samples were frozen until analysis.

To measure variation in arthropod numbers throughout the day, a series of pitfall and sticky board samples were taken at intervals of three hours during 24 h periods. Such samples were taken in two years on six days in total: in 1995 on 15 June, 26 June and 16 July, and in 1996 on 7 July, 15 July and 27 July.

The number of arthropods caught reflects their activity. Motion makes a potential arthropod prey item more visible, and hence more available, but possibly more difficult for a chick to catch (Schekkerman & Boele 2009: wind and temperature negatively affected ingestion rate). Schekkerman *et al.* (2003) found that growth of red knot chicks (*Calidris canutus*) in Siberia varied in parallel with both weather-induced and seasonal variation in arthropod availability. Similarly, Tulp *et al.* (2004) showed that growth rate of Siberian chicks of little stint (*Calidris minutilla*), especially at young ages, was correlated positively with the number of arthropods caught. Similarly, thus, the biomass of arthropods caught on sticky boards and in pitfall traps likely reflects actual food availability for the chicks, and thus can be used to evaluate variation in food availability with season and weather.

Identification of food items

Arthropods encountered on sticky boards and in pitfall traps were counted and identified to family level, using a dissecting microscope and an identification guide (Borror & White 1970). Length of each insect was measured to the nearest mm. Families of arthropods encountered were combined into several groups, based largely on relevance as food source, and on physical dimensions. Because adults and larvae of chironomids (Diptera: Chironomidae) form an important food source for waders, as do mosquitoes (Culicidae) and midges (Ceratopogonidae), they were quantified separately from the other Diptera encountered, and were combined as a group with the name "Nematocera". Thus, the group Nematocera, although belonging to the order of Diptera, is here specified as a separate group containing mosquitoes, midges (of which many are Chironomidae), and crane flies (tipulids). The group of other "Diptera" contains all flies, excluding the Nematocera. Although black flies (Simuliidae) are part of the Nematocera, we classified them with the other dipterans, because of their larger body size. Other groups that we distinguished are Araneidae, Hymenoptera, Hemiptera, Homoptera, Lepidoptera (butterflies and moths), Trichoptera, Orthoptera, Coleoptera, and Collembola. Larvae caught in pitfalls belonged to Lepidoptera and Coleoptera, and were classified as larvae of those two orders.

Environmental temperature

To relate arthropod abundance to climatic conditions, we recorded environmental temperatures continuously throughout the season. A white and a black copper sphere, each having a diameter of 3.5 cm and containing a centrally positioned thermocouple, were positioned 10 cm above the ground in a microhabitat characteristic of foraging shorebird chicks, in low vegetation dominated by lichen, low sedges and small willows (<10 cm). The white sphere provided a measure of ambient air temperature (T_a), with the effects of wind and solar radiation largely factored out. The black sphere provided an approximation of the thermal environment with wind and solar radiation factored in, although not necessarily in the same fashion as experienced by the chick (Bakken *et al.* 1985, Walsberg & Weathers 1986). By subtracting white-sphere temperature from black-sphere temperature, we obtained a measure of radiative-convective load independent of T_a. These estimates correlated well with levels obtained for comparison with a pyranometer ($r^2 = 0.84$, $F_{1,\,117} = 623$, $P < 0.0001$; LI-200SA, Lincoln, NE, USA). Wind speed was measured 10 cm above the ground with a cup anemometer (A100L2, Grant Instruments Ltd., Barrington, England; minimum threshold 0.15 m s^{-1}). Local climate data were averaged over 15-min intervals and recorded with a Squirrel 1204 data logger (Grant Instruments Ltd., Barrington, England).

Analysis

Lengths of arthropods were converted to dry mass using the equation mass = $0.00305 \times \text{length}^{2.62}$ (mg dry mass, mm) (Rogers *et al.* 1976), which is valid for arthropods between 0.5 and 36 mm in length. The majority of arthropods collected fell within this range. Given the linearity of the allometric relationship between length and dry mass, and that few insects were outside the prediction range, estimates of total mass are reasonably unbiased.

Statistical analyses were performed using SPSS version 12 (SPSS Inc. 2003). Numbers and biomass of arthropods caught with individual sticky boards and pitfall traps were averaged to one value for sticky boards and one for pitfall traps per habitat type (dry or wet) per collection interval (24 h or 3 h). Thus, each value is based on six traps. Data were log-transformed prior to statistical analysis. Total number and total dry mass of arthropods caught correlated strongly (partial correlation for four years on log-transformed data: $r_{81} = 0.93$, $P < 0.0001$), and biomass was therefore used as index of arthropod availability in the statistical analysis.

Table 3.1. Orders and families of arthropods encountered on sticky boards and in pitfalls in 1995 & 1996.

order	% of total	family	common name
Collembola	1.4		springtails
Orthoptera	0.1	Acrididae	grasshoppers
		Tetrigidae	pygmy grasshoppers
Hemiptera	0.6	Cicadellidae	
		Cercopidae	froghoppers and spittlebugs
Neuroptera	0.0		lacewings
Lepidoptera	0.4	Nymphalidae	brushfoots
		Pieridae	sulfurs and whites
		Noctuidae	(moth)
		Arctiidae	tiger moths
		Notodontidae	(moth)
		Hesperiidae	skippers
		Geometridae	(moth)
Trichoptera	0.1		caddisflies
Diptera	78.2	Syrphidae	hover flies
		Tabanidae	horse flies & deer flies
		Simuliidae	black flies
Nematocera	11.8	Tipulidae	crane flies
		Culicidae	mosquitoes
		7 families of midges	midges (incl. Chironomidae)
Hymenoptera	2.2	Ichneumonidae	parasitic wasps
			sawflies
		Vespidae	wasp
		Formicidae	ants
		Apidae	bumble bees
Coleoptera	0.4	Carabidae	ground beetles
		Scarabaeidae	scarab beetles
		Silphidae	carrion beetles
		Elateridae	click beetles
		Chrysomelidae	leaf beetles
		Cerambycidae	long-horned beetles
		Curculionidae	weevils
		Cantharidae	soldier beetles
		Dytiscidae	
Ephemeroptera	0.0		mayflies
Acari	0.0		mites
Aranae	4.8	Lycosidae	wolf spiders
		Thomisidae	crab spider
		Attidae?	

Results

Taxa
For samples collected in 1995 and 1996, arthropods were identified to family level. In total, 38 families were collected from 12 orders (table 3.1). Diptera, *i.e.* flies, were the most common group throughout the season (78% of total number; fig. 3.1) followed by mosquitoes, chironomids, crane flies and midges (together 12%). Within the Coleoptera, 9 species in 7 genera were encountered (table 3.2).

Abundance
To analyse abundance of food items, we combined arthropods that were trapped in pitfalls and on sticky boards. Although this might bias the sample towards either flying or crawling arthropods, the data were handled the same way for all the samples and thus are comparable. In addition, we reported trap results separately as well. Chicks forage on arthropods present both on the soil and in the vegetation, so both ground-dwelling arthropods such as beetles and spiders caught in pitfalls and flying insects such as flies and mosquitoes caught on sticky boards form relevant aspects of their diet. Mean daily dry biomass was 114 mg day^{-1} trap^{-1} (n = 84, sd = 89.0) and varied between 0 and 424 mg. The number of arthropods averaged 49 day^{-1} trap^{-1} (n = 84, sd = 39.7) and varied between 0 and 165. Variation in abundance was large: five-fold differences between samples were common and the maximum difference between samples was 170-fold. The average dry mass (mg day^{-1} trap^{-1}) was relatively consistent between years: 114 in 1995 (n = 41, sd = 91.7), 131 in 1996 (n = 15, sd = 107.0), 98 in 1997 (n = 16, sd = 77.5), and 112 in 1998 (n = 12, sd = 75). The number of individuals averaged 6 day^{-1} trap^{-1} in pitfall traps, with an average dry mass of 23 mg day^{-1} trap^{-1}. On sticky boards, arthropods averaged 47 per trap each day, having an average dry mass of 97 mg day^{-1} trap^{-1}.

Table 3.2. Genera and species encountered in/on traps in 1995 and 1996, in the family of Coleoptera (Borror & White 1970), as well as the number caught of individuals of each species.

genus	species	nr individuals
Agonum	*affine*	3
Amara	*alpina*	10
Bembidion	(unknown)	10
Cymindis	*planipennis*	1
Dyschirius	*hiemalis*	16
Elaphrus	*lapponicus*	10
Pterostichus	*brevicornis*	16
Pterostichus	*caribou*	82
Pterostichus	*punctatissimus*	144

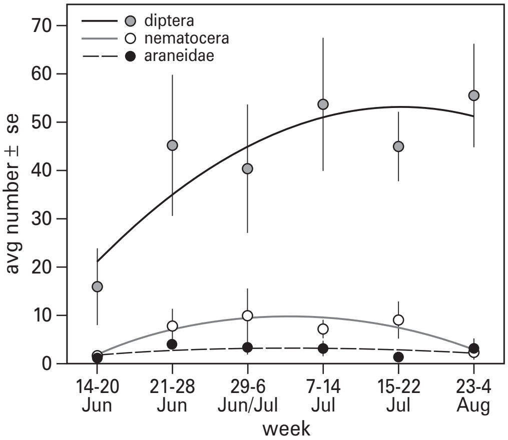

Figure 3.1. Seasonal pattern in abundance of the most common species groups: Diptera, Nematocera and Araneidae. Number given is the number caught per pitfall trap plus sticky board combined, shown for each week. Lines are quadratic functions fitted to lead the eye. Diptera were most abundant in the traps.

Variation through season
Insect numbers peaked between the end of June and the end of July (fig. 3.2). Insects caught on sticky boards showed a marked seasonal pattern; captures in pitfalls were less variable through the season. Because numbers caught on sticky boards exceeded those in pitfalls, the pattern from the sticky boards dominates the

overall pattern. Total mass increased, more slowly than the increase in numbers, to a peak around mid-July, a few days later than the peak in numbers (fig. 3.2). The pattern was roughly similar for 1995 through 1998 (fig. 3.3). The increase in mass through a large part of the season was due mainly to the fact that larger insects peaked later in the season (fig. 3.4). The smallest insects reached maximum numbers earliest in the season and had the broadest peak, continuing from the end of June to the end of July. Larger species reached maximum numbers later in the season and had a narrower peak. A similar but less marked pattern was evident in number of arthropods caught in pitfall traps.

Total mass (log-transformed) of arthropods caught increased at higher ambient temperatures (GLM: T_a: $F_{1,\,39} = 14.7$, $P < 0.001$, $r^2 = 0.27$). Wind speed had a negative effect on mass

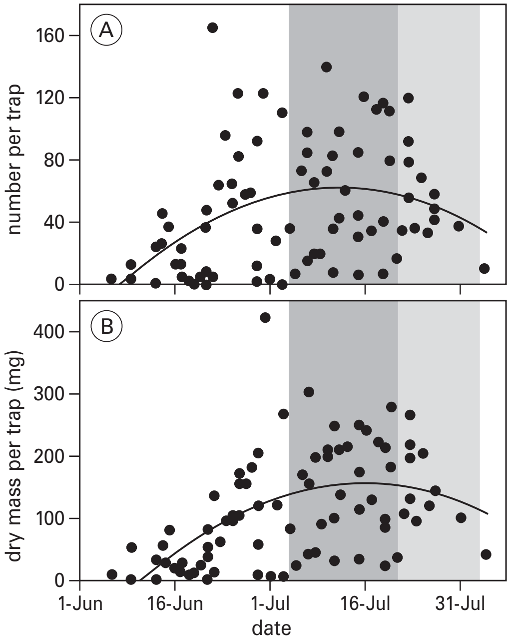

Figure 3.2. Seasonal pattern in number (upper graph) and mass (lower graph) of arthropods caught on sticky boards. Values given are average number/mass per sticky board and pitfall trap combined, for 1995–1998, shown for each day. Lines are quadratic functions fitted to lead the eye. Shaded areas reflect the periods from mean hatching date of chicks (4 July) to early age of sustained flight of small shorebird species (17 d in least sandpiper and dunlin; dark grey) up to the later age of sustained flight of larger shorebird species (30 days in whimbrel and Hudsonian godwit; light grey). Dashed vertical line reflects mean onset of shorebird egg incubation, ca. 20 days prior to hatching date.

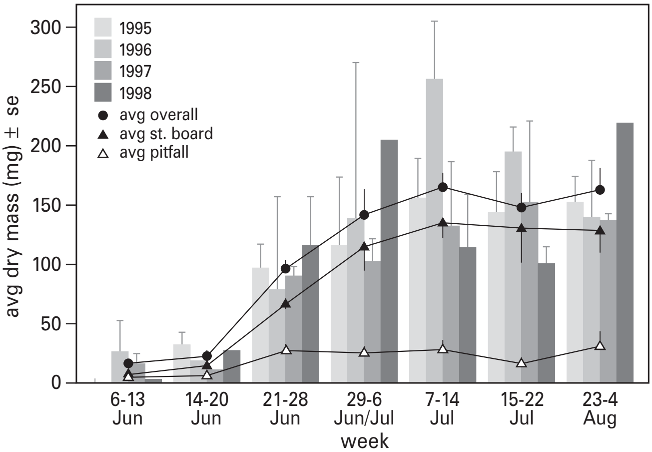

Figure 3.3. Variation between years in arthropod abundance. Value is dry mass caught per pitfall trap and sticky board combined, shown for each week. For comparison, overall averages are shown as well for overall mass, mass on sticky boards, and mass in pitfalls.

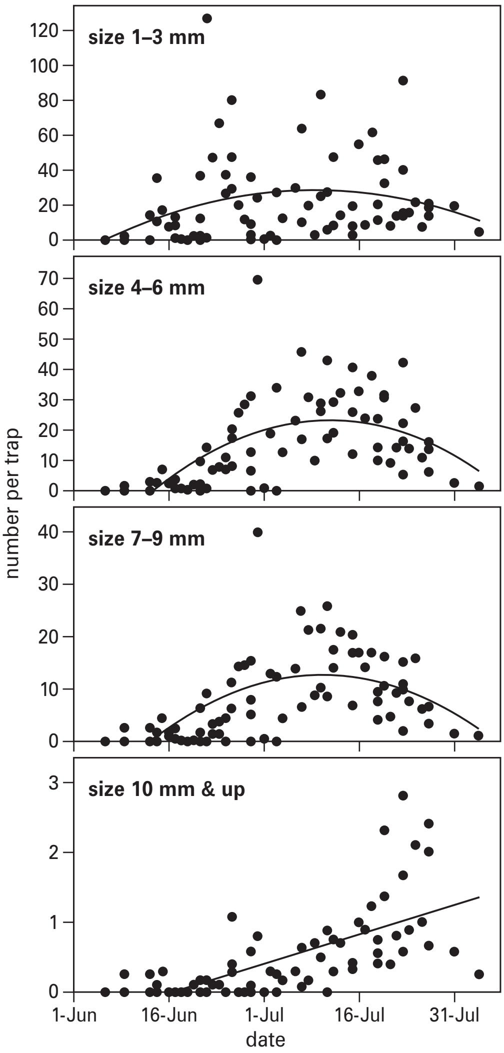

Figure 3.4. Variation in abundance between smaller and larger species of arthropods. The vertical axis is the number caught per sticky board only, for 1995-1998, shown for each day. Lines are quadratic functions fitted to lead the eye. Note the difference in scale. Larger species emerged later, in lower numbers, and during a briefer period of time.

caught, especially in conjunction with low ambient temperatures (model after entering wind as well as T_a: $F_{3,\,37} = 13.2$, $P < 0.001$, $r^2 = 0.52$; the effects of both wind and the interaction of wind×T_a were significant, $P < 0.001$). In addition to the effects of wind and temperature, inclusion of date after entering Ta and wind further improved the model (final model: $F_{4,\,36} = 21.4$, $P < 0.001$, $r^2 = 0.70$), indicating a seasonal trend in arthropod availability, independent of weather conditions. Weather conditions did not affect smaller arthropods differently than larger arthropods.

Daily pattern

Both number of individuals and mass of arthropods caught were highest during daytime, between late morning (11:00) and early evening (20:00) (fig. 3.5). The numbers of flying insects caught on the sticky boards exhibited a stronger diurnal pattern than the arthropods caught in pitfalls (fig. 3.5). The high number of insects caught during daytime was related to the abundance of dipterans, which were almost exclusively caught between 11:00 and 20:00 (fig. 3.6). Nematocerans were caught mostly at night (02:00 sample), whereas during daytime numbers of this group showed a minimum in both pitfalls and on sticky boards (fig. 3.6). Nematocerans were the principal group of arthropods caught at night. Biomass varied less between day and night than numbers caught, and was more similar between pitfalls and sticky boards (fig. 3.5). Abundance throughout the day was unrelated to size groups. Both overall mass and overall numbers of arthropods caught on sticky boards and pitfalls combined, showed a small but significant increase with ambient temperature and radiation (GLM on log-transformed data: ambient temperature: slope = 0.035 ± se = 0.009, $F_{1,\,44} = 15.0$; $P < 0.001$, radiation: slope = 0.05 ± se = 0.017, $F_{1,\,44} = 9.3$, $P < 0.005$; no interaction; $r^2 = 0.35$). The same correlation was found for the total number of dipterans (GLM on arcsine-transformed numbers: ambient temperature: $F_{1,\,44} = 8.7$; $P < 0.005$, radiation: $F_{1,\,44} = 43.1$, $P < 0.001$, no interaction; $r^2 = 0.53$). Numbers tended to decrease with wind speed at 10 cm above ground, but this effect was not significant.

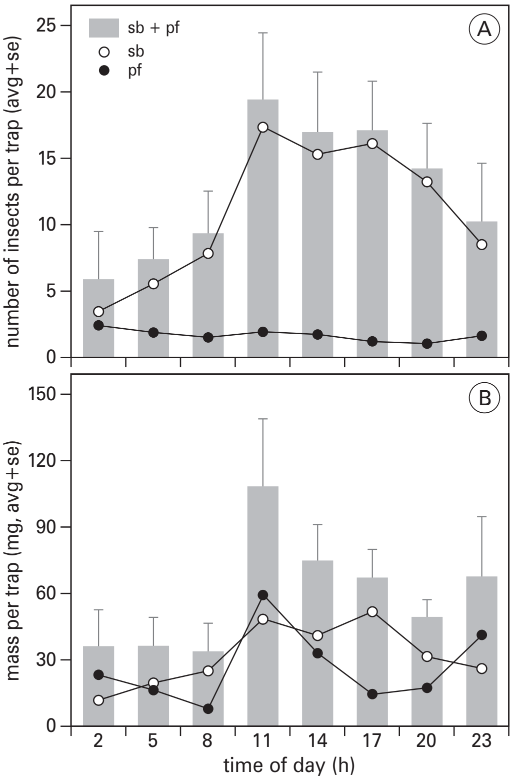

Figure 3.5. Diurnal pattern in arthropod abundance. Shown are the number and dry mass found on sticky boards and pitfalls combined (bars, + se), and the number found on sticky boards and in pitfalls separately (circles). Only the 02:00 sample was collected during hours of darkness (midsummer twilight: 23:30-1:45). Highest numbers were caught at 11:00 h.

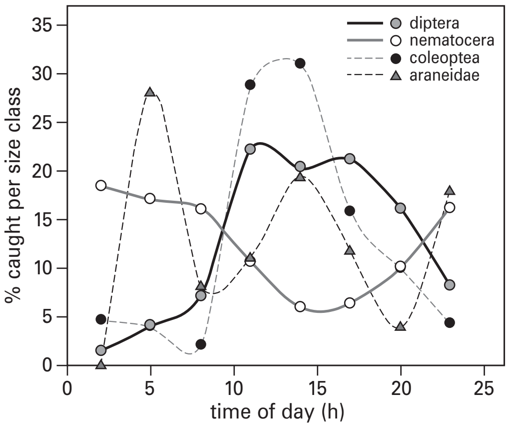

Figure 3.6. Diurnal activity patterns of the most common arthropod species groups, shown as the percentage of the total number caught during the 24-h period. Values reflect numbers caught in sticky boards and pitfalls combined. Diptera were mostly active during day, Nematocera during night.

Discussion

High insect abundance with regard to chick growth

In polar regions, arthropod abundance follows a clear seasonal pattern with a peak abundance in the summer season, in response to favourable environmental conditions (Danks 1999). Patterns similar to that reported in this paper for Churchill were reported in other arctic studies (e.g. MacLean & Pitelka, 1971, at Barrow in Alaska; Tulp & Schekkerman, 2008, at Taimyr in Siberia). Latitude and environmental conditions related to latitude, do however result in a large variation between polar study sites in duration and timing of arthropod availability.

At Churchill, which lies at a lower latitude than Barrow, the peak in food availability was longer than at Barrow. At Churchill, arthropod numbers and biomass started to increase by mid-June and were starting to decrease again only by the end of July, leaving a period of 35-40 days with high food availability. Chicks at Churchill hatched mostly in the first week of July, meaning that those chicks that need the most time to fledge (such as slow-growing golden plovers and the larger whimbrel and Hudsonian godwit: 24–30 days; Cramp 1998, Jehl 2004), reached sustained flight by the end of July or early August (Jehl 2004, chapter 2). This is within the period of peak food availability.

At Barrow, the period with high arthropod numbers was ca. 15 days shorter than at Churchill. Numbers generally did not start to increase before the beginning of July, and were decreasing again between 20–25 July, leaving a period of only 20–25 days with high food availability for chicks (MacLean & Pitelka 1971). This shorter period gives the larger and more slowly growing species that breed there, such as Hudsonian godwit, whimbrel and golden plover (Johnsgard, 1981), barely enough time to complete growth. Because mean hatching date at Barrow also seems to be slightly later than at Churchill (5–15 July, Holmes 1966a, but note difference in years and changed that may be related to that), these chicks will have reached the age of sustained flight by early to mid-August, which is well after the peak in food availability. Possibly, late in the season the chicks at Barrow resolve this by feeding more on insect larvae, which are available until late August, as was shown for dunlin (Holmes 1966a).

Thus, at Churchill the period of high food availability is more than sufficient for even the chicks of larger and more slowly growing species to complete growth. Only at more northern latitudes does the brevity of the period during which food is available become limiting, emphasizing the need for rapid chick growth, in particular for the larger, generally more slowly growing species.

Interestingly, of the shorebird species that we studied, golden plovers have the most northerly distribution (as far north as Banks, Victoria, Melville and Devon Islands, Northwestern passages; Godfrey 1966), and the species is near its southern limit at Churchill. This species grows relatively slowly for its size and needs approximately 24 days to reach sustained flight. Even at Barrow, the peak in food availability is barely long enough to cover this period. At more northerly regions this peak will only become shorter, which will make it challenging for the chicks to complete growth in time.

Size of insects with regard to chick growth

At the time the chicks hatch at Churchill (first week of July; Jehl 2004, chapter 2), even though arthropod biomass has not yet reached its peak, smaller insects already occur in high numbers. These small insects are particularly suitable prey for the youngest chicks, which cannot handle larger food items efficiently (Schekkerman & Boele 2009). When the chicks have grown and require more energy, they can feed on the larger insects that become more abundant later in July and require less handling time than an energetically comparable number of smaller prey items ((Baker 1977, Zwarts & Wanink 1993). The increase in size of arthropods in the course of the season was reported also for Taimyr, Siberia (Tulp & Schekkerman 2008).

Insect abundance compared to other latitudes

Arthropod abundance at Churchill averaged 114 mg dry mass and 49 arthropods per day per sticky board plus pitfall trap. This equaled or exceeded arthropod abundance at shorebird breeding locations at both lower and higher latitudes, in studies where comparable insect trapping methods were used. Per pitfall trap, we caught 6-7 arthropods or 23 mg dry mass per day on average throughout the season. In the Netherlands these numbers were 19 mg day^{-1} trap^{-1}; in Sterlegova, Siberia: 7 arthropods or 12 mg per day per trap (Schekkerman *et al.* 2003); in Taimyr, Siberia (close to Sterlegova): 4–9 arthropods or 15–30 mg per day per trap (Tulp & Schekkerman 2008). Schekkerman (2008) reported that in Greenland 2–13 arthropods were caught on average per day (own data and Rasch & Caning 2004), which is in the same range as the number caught in Churchill. The type of food was comparable between Churchill and more northern latitudes, dipterans being the most abundant group encountered in both our study and the studies in Alaska and Siberia (McLean & Pitelka 1971, Schekkerman *et al.* 2003).

Diurnal patterns in insect abundance and chick foraging behaviour

Both numbers and total biomass of arthropods caught were higher during daytime than at night, and peaked between late morning and early evening. Variation in arthropod abundance over the day largely reflects the ecology of each taxonomic group. Nematocera (mostly mosquitoes and chironomids), for example, were mostly active during nighttime hours, when temperatures were lowest. This is typical for mosquitoes and chironomids, which remain relatively inactive during the day (Boyd 1930, Crans 1989). In contrast, Diptera, defined in this study as black flies, horse flies and hover flies, are mostly diurnal (e.g., black flies; Simuliidae web pages at blackfly.org.uk).

Some insects, including mosquitoes, are thought to be attracted to yellow, the colour of the sticky boards used in this study. This could explain the generally higher catches of insects on sticky boards during the day. However, two findings suggest that this was not the case. First, apart from Nematocera, arthropods caught in the pitfalls showed a similar pattern as those caught on the yellow sticky boards. Second, Nematocera were mostly caught during nighttime, when colours are less apparent.

Foraging golden plover chicks depend on vision to locate prey, and their foraging activity was restricted to daylight hours (Krijgsveld *et al.* 2003b; chapter 6) when food also was more abundant. They increased the length of their foraging bouts markedly between 6:00 and 11:00 h, even though food availability was lower than it was after 11:00 h. In addition, lower ambient temperatures, which reduce foraging bout lengths (Krijgsveld *et al.* 2003a,b, chapters 6 & 7), generally occurred in the morning rather than in the afternoon. A similar pattern was found in the Netherlands for godwit chicks, which ingested most prey in the morning and evening (Schekkerman & Boele 2009).

High hunger levels in the early morning may drive the chicks to increase their foraging effort beyond the level that would be expected based on the limited food availability. Thermoregulatory costs of extended foraging at lower ambient temperatures apparently are not high enough to preclude such behaviour. Wind speeds also tended to be lower in the morning and evening hours than during the afternoon (chapter 1). Higher wind speeds reduce the number of arthropods caught in traps and make foraging more difficult (Schekkerman & Boele 2009). Higher ambient temperatures also make catching prey more difficult (Schekkerman & Boele 2009), but increased the number of arthropods caught in traps. Low wind speed and ambient temperature in the morning hours might thus increase the accessibility of individual arthropods while reducing their numbers in traps, making foraging more favorable relative to trap results. The intake rate of prey might actually be higher than in the afternoon, especially when insects are merely inactive at cooler temperatures rather than less abundant.

In summary

Numbers of arthropods in Churchill were high compared to other areas in the arctic, and were available during the entire breeding season, providing good feeding conditions for shorebirds that were breeding in high densities in the area. Low winds and high ambient temperatures increased the numbers of arthropods caught in traps. However, foraging activity of chicks probably is related not only to variation in abundance of prey, but also to the ease of prey capture and to diurnal patterns in hunger level of the chicks. Spells of unfavourable weather may suppress food availability and hence growth.

Acknowledgements

Adrienne Smith skillfully analyzed large quantities of insect samples. We thank Quinten van Katwijk, Jeroen Reneerkens and Gabe McNett for helping to collect samples, especially in the nighttime hours when mosquitoes were plentiful and polar bears lurking. The Churchill Northern Studies Centre provided us with all the support we needed. Simon Verhulst provided useful comments to the manuscript. This study was financed by National Science Foundation grant OPP-9423522 awarded to RER and G. Henk Visser. This paper is dedicated to the memory of Henk Visser.

Part 2

Physiological adaptations: growth rate versus functional maturity

Chapter 4

Catabolic capacity of the muscles of shorebird chicks: maturation of function in relation to body size

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Physiological & Biochemical Zoology 74: 250–260 (2001)

Abstract

Newly hatched precocial chicks of arctic shorebirds are able to walk and regulate their body temperatures to a limited extent. Yet, they must also grow rapidly to achieve independence before the end of the short arctic growing season. A rapid growth rate may conflict with development of mature function, and because of the allometric scaling of thermal relationships, this trade-off might be resolved differently in large and small species. We assessed growth (mass) and functional maturity (catabolic enzyme activity) in leg and pectoral muscles of chicks aged 1–16 d and adults of two scolopacid shorebirds, the smaller dunlin (*Calidris alpina*: neonate mass 8 g, adult mass 50 g) and larger whimbrel (*Numenius phaeopus*; neonate mass 34 g, adult mass 380 g). Enzyme activity indicates maximum catabolic capacity, which is one aspect of the development of functional maturity of muscle. The growth rate–maturity hypothesis predicts that the development of catabolic capacity should be delayed in faster-growing muscle masses. Leg muscles of both species were a larger proportion of adult size at hatching and grew faster than pectoral muscles. Pectoral muscles grew more rapidly in the dunlin than in the whimbrel, whereas leg muscles grew more rapidly in the whimbrel. In both species and in both leg and pectoral muscles, enzyme activities generally increased with age, suggesting increasing functional maturity. Levels of citrate synthase (CS) activity were similar to those reported for other species, but l-3-hydroxyacyl-CoA-dehydrogenase (HOAD) and pyruvate kinase (PK) activities were comparatively high. Catabolic capacities of leg muscles were initially high compared to those of pectoral muscles, but with the exception of glycolytic (PK) capacities, these subsequently increased only modestly or even decreased as chicks grew. The earlier functional maturity of the more rapidly growing leg muscles, as well as the generally higher functional maturity in muscles of the more rapidly growing dunlin chicks, contradicts the growth rate–maturity function trade-off and suggests that birds have considerable latitude to modify this relationship. Whimbrel chicks, apparently, can rely on allometric scaling of power requirements for locomotion and the thermal inertia of their larger mass to reduce demands on their muscles, whereas dunlin chicks require muscles with higher metabolic capacity from an earlier age. Thus, larger and smaller species may adopt different strategies of growth and tissue maturation.

Introduction

Shorebird chicks growing on the arctic tundra are faced with a climatically variable environment and a short season to complete their development. Being precocial, the chicks forage by themselves and, thus, are strongly affected by environmental conditions. Their thermoregulatory capacities develop rapidly (Visser & Ricklefs 1993b; JB Williams & RER, unpublished data), but during the first days after hatching, the chicks can produce heat and maintain their own body temperatures only to a limited extent. Thus, as small chicks forage they lose body heat, and their parents must brood the chicks at regular intervals to rewarm them. Time devoted to brooding cannot be used for foraging by either the chick or the parent. For chicks, the reduced time for foraging can depress growth rate, especially during adverse weather conditions (Beintema & Visser 1989b). If chicks could increase their thermoregulatory capacities at a given age or size, they would increase the proportion of the day available for feeding.

Thermoregulatory capacity in birds depends on the functional maturity of the skeletal muscles, which, apparently, are the primary source of heat production in response to cold stress in both adult (Dawson 1975; Hohtola & Stevens 1986) and young (Olson 1994; Marjoniemi & Hohtola 1999) birds. However, development of functional maturity also imposes costs. Several authors have suggested that a trade-off exists between functional capacity and growth rate (Dawson & Evans 1957; Ricklefs 1979; Ricklefs andWebb 1985; Olson 1992; Choi *et al.* 1993; Ricklefs *et al.* 1994; Dietz & Ricklefs 1997; Pearson 1998; Starck & Ricklefs 1998). For example, Shea *et al.* (1995) showed that functional maturity, indicated by dry matter content and pyruvate kinase (PK) activity of muscles, was lower in a line of Japanese quail (*Coturnix coturnix japonica*) chicks selected for higher growth rate than in nonselected chicks. To the extent that energy, nutrients, and tissues allocated to mature function cannot be allocated to growth, investment in mature function reduces growth rate.

If a trade-off existed between growth rate and functional maturity, it is plausible that this compromise would be resolved differently by chicks of small and large species. The body size of a precocial neonate influences its relationship to the thermal environment during the growth period (Visser & Ricklefs 1993a), and adult body size is also correlated with the rate of postnatal growth and development (Ricklefs 1979; Starck & Ricklefs 1998). Chicks of smaller species have high surface-to-volume ratios and, therefore, lose heat rapidly to their surroundings. Chicks of larger species have more favorable thermal relationships to their environments but, typically, have relatively long developmental periods. Small species could increase functional maturity to increase foraging time, but it is unclear whether the resulting increased energy intake would more than balance their increased energy expenditure for locomotion and body temperature regulation. Large species could decrease functional maturity to accelerate growth, but this might impose a cost in that it reduces foraging time and, therefore, energy intake more than it reduces the energy requirement of growth. Measurements of mass increase show that relative growth rates of shorebird chicks vary inversely with adult body mass (Ricklefs 1968; Beintema & Visser 1989a). Accordingly, we would predict that smaller species would exhibit lower functional maturity, having resolved the growth rate–maturity trade-off in favor of rapid growth and increased dependence on parental care for thermoregulation early in development.

In this study, we explored functional maturity and growth rate in chicks of two species of shorebirds that differ in size. We selected one small and one large shorebird, both belonging to the family Scolopacidae: the dunlin (*Calidris alpina*: neonate mass 7.7 g [chapter 2]; adult mass 50 g [Jehl & Murray 1986]) and the whimbrel (*Numenius phaeopus*: neonate mass 33.5 g [chapter 2], adult mass 380 g [Dunning 1993]). We assessed ontogenetic changes in the functional maturity of muscle by measuring the activities of three key catabolic enzymes: citrate synthase (CS), l-3-hydroxyacyl-CoAdehydrogenase (HOAD), and pyruvate kinase (PK). Activities of catabolic enzymes indicate the capacity of muscle to generate ATP, which is necessary for sustained shivering thermogenesis and locomotion (Marsh and Wickler 1982; Newsholme & Crabtree 1986; Olson 1990; Bishop *et al.* 1995). We also weighed chicks and their principal muscle groups and related measures of muscle biochemistry and size to the metabolic scope of chicks in response to cold stress. Thus, we could characterize and relate functional maturity of skeletal muscles, growth rate, and whole-organism function. In the general context of the growth rate–maturity hypothesis, we also address the use of each catabolic pathway at different times during development, the roles of leg and pectoral muscles in the development of endothermic capacity, and the influence of body size on the course of maturation in skeletal muscle function.

Materials and methods

Animals

Whimbrel and dunlin eggs were collected on the tundra near Churchill, Manitoba, Canada, in June–July 1996 and 1997. After hatching in an incubator, chicks were kept in boxes fitted with lightbulbs to provide a range in air temperatures between 25° and 38°C. Thus, the chicks could select a preferred thermal environment. When the chicks were homeothermic, they were kept at ambient room temperature (18°–25°C). Chicks stood on a 0.5 cm^2 wire-mesh cloth floor elevated above a layer of sawdust placed on the floor of the boxes for hygiene and easy cleaning. All chicks were provided food and water ad lib. Food consisted of pheasant starter type 2 mix (Spelderholt, Beekbergen, Netherlands; 1996) or a comparable turkey prestarter mix (Puratone, Niverville, Manitoba; 1997), supplemented with a mix of canned tuna, boiled eggs, and freshly caught mosquitoes. Adult birds were trapped or shot in July near Churchill and were sampled immediately. Collecting was carried out under permit from the Canadian Wildlife Service. Husbandry and laboratory procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri–St. Louis.

Growth analyses

Estimates of growth parameters were obtained by nonlinear curve fitting of the Gompertz equation. Parameters for body mass growth were based on daily weighings of 54 chicks that were pen reared in Churchill from 1995 to 1998 (chapter 2). Mean body masses for each day of age were log transformed and fitted by nonlinear regression to the logarithmic form of the Gompertz equation:

$$\ln [W(t)] = \ln A - \exp[-K(t-t_i)],$$

where W(t) is the mass (g) at age t (d), A is the asymptote or growth plateau (g), K is the growth rate constant (d^{-1}), and t_i is the inflection point of the growth curve (d). The Gompertz equation fit the data more closely than either the von Bertalanffy or logistic growth models (Ricklefs 1967). In this analysis, asymptotic body masses were set at 50 g for the dunlin (Jehl & Murray 1986) and 380 g for the whimbrel (Dunning 1993). Growth parameters for pectoral and leg muscle growth were based on the fresh muscle masses of the 12 whimbrel and 12 dunlin chicks that were killed (see below). Parameters were estimated by fitting one growth curve to all data, with standard errors being asymptotic values returned by the NLIN procedure of SPSS (version 7.5 for Windows).

In addition, we calculated exponential growth rates (EGR) for pectoral and leg muscles over each age interval as the logarithmic growth increment divided by the age interval:

$$EGR = [\ln(W_f)-\ln(W_i)] / (f-i),$$

where W_i is the initial mass (g), W_f is the final mass (g), and $(f-i)$ is the interval (d) between samples. Average values were used at each age. Poor growth in one of the whimbrel chicks at 12 d induced a large variance in the exponential growth rate. Accordingly, we averaged the growth increment from 8 to 16 d in both muscles. The standard error of EGR was estimated as the square root of the variance in EGR, which is equal to $[var(W_f)+var(W_i)]/(f-i)$, divided by the square root of the sample size. According to the Gompertz model of growth, the exponential growth rate decreases linearly with the logarithm of size, that is, $[\ln(W_i)+\ln(W_f)]/2$. Thus, the Gompertz growth constant is the slope relating the exponential growth rate to $\ln(W/A)$ (Ricklefs *et al.* 1994; see also fig. 4.3). Due to small sample sizes, differences in EGR could not be tested statistically.

Tissue preparation

We collected muscle samples from 1-, 2-, 4-, 8-, 12-, and 16-d-old chicks and adult dunlin and whimbrel, with a sample size of 2 at each age. We restricted our measurements to the first 16-d posthatch because of the high relative growth rates and the large changes in thermoregulatory capacities during this period. All birds were killed by cervical dislocation or CO_2 asphyxiation. Birds were weighed to the nearest 0.1 g and transferred immediately to a glass plate chilled on ice. For the biochemical measurements, the left pectoral muscle (*Musculus pectoralis pars thoracicus*) and all of the muscles of the left leg below the hip were dissected, carefully removing nonmuscle tissue as much as possible. Excised tissues were weighed to the nearest 0.1 mg. These masses were multiplied by 2 to obtain the total masses of the muscles. After weighing, tissues were returned to a second glass plate maintained on ice, minced, and stored in tightly sealed 1.0 mL InterMed NUNC cryotubes. All tissue samples were frozen in liquid nitrogen within 15–25 min of death. Samples were shipped to Villanova University, PA on dry ice and stored at –80°C until assayed. Independent measurements established that the activities of at least CS and HOAD are unaffected by the typical handling time in this study (O'Connor & Root 1993) or by storage at –80°C for periods of up to 4 months (Olson *et al.* 1988).

Assays of enzymatic activities

We measured the activity of CS (EC 4.1.3.7), HOAD (EC 1.1.1.35), and PK (EC 2.7.1.40) under saturating substrate concentrations. All three are regulatory, nonequilibrium enzymes and were used to indicate the capacity for flux through the major catabolic pathways (Newsholme & Crabtree 1986). The activities of the enzymes indicate the maximum capacity for flux and not the actual flux through the respective catabolic pathways. CS catalyzes the condensation of acetyl CoA and oxaloacetate in the tricarboxylic acid (TCA) cycle. CS activity reflects the capacity for flux through the TCA cycle and, therefore, provides an index of aerobic capacity (Fitts *et al.* 1975; Hochachka *et al.* 1977). HOAD catalyzes the formation of ketoacyl CoA in the β-oxidation pathway for the breakdown of fatty acids, and HOAD activity indicates the capacity for lipid catabolism (Bass *et al.* 1969). PK catalyses the conversion of phosphoenolpyruvate (PEP) to pyruvate in the glycolytic pathway. The activity of this enzyme provides an index of the glycolytic capacity (Newsholme & Leech 1983).

On the day of the assay, the minced muscle was thawed on ice, weighed, and homogenized in 10 volumes (unless a limited amount of tissue required a higher dilution) of 100 mM potassium phosphate buffer with 2 mM EDTA (pH 7.3 at 0°C) using a glass-glass homogenizer. For the assays of CS and HOAD activity, homogenates were sonicated with a Branson Sonifier equipped with a microtip for three 15-s intervals separated by 45-s pauses. All samples and homogenates were maintained on ice during homogenization and sonication and until assayed to prevent thermal denaturation.

The activities of CS, PK, and HOAD were assayed spectrophotometrically on a Gilford response spectrophotometer at 25.0°C. Each assay was replicated at least once. All assays were performed in a final medium of 1 mL. Absorbance was measured for 6 min before adding the final substrate to allow time for thermal equilibration and for a control rate to be measured. Subsequently, the absorbance was measured for 5 min. CS activity was measured at 412 nm, according to a modification (as used by Olson 1990) of the protocol of Srere (1969). The reaction medium contained 200 mM Tris-HCl, 5 mM EDTA, 0.1 mM 5,5´-dithiobis (2-nitrobenzoic acid), 0.2 mM s-acetyl CoA, 0.5 mM cis-oxaloacetate, and 0.1 mL diluted homogenate, pH 7.3 (at 25°C). The reaction was started by adding the oxaloacetate. HOAD activity was measured at 340 nm, according to a modification (Olson 1990) of the method of Bass *et al.* (1969). The reaction medium contained 100 mM triethanolamine-HCl, 5 mM EDTA, 0.225 mM NADH, 0.1 mM s-acetoacetyl CoA, and 0.1 mL diluted homogenate, pH 7.0. The reaction was started by adding the s-acetoacetyl CoA. PK activity was measured at 340 nm. The reaction medium contained 80 mM Tris-HCl, 100 mM KCl, 10 mM $MgCl_2$, 2 mM PEP, 5 mM adenosine 5´-diphosphate, 0.15 mM NADH, 0.10 mM D-fructose 1,6-diphosphate trisodium salt, 5 units LDH, and 0.1 mL diluted homogenate. The reaction was begun by adding the PEP. Throughout the text, activities are expressed as micromoles of substrate converted per minute per gram fresh tissue, or international units per gram.

Statistics
All data on adult birds were excluded from statistics. Statistics were performed using SPSS statistical software version 7.5. Tests were performed as much as possible within a single model, using general linear models (GLM). Age was entered in the models as a covariate or as a random factor, depending on the linearity of the data, and body mass was entered as covariate. Species and tissue type were entered as fixed factors. For all tests, individual data were used.

Results

Growth
Dunlin chicks grew more rapidly than whimbrel chicks. At 16 d of age, the dunlin chicks had nearly reached adult body mass, whereas the whimbrel chicks were only half grown. As a result, the growth rate constant (K) for body mass in dunlin chicks exceeded that for whimbrel chicks by 50% (*t*-test: $t_{52} = -10.7$, $P < 0.0001$), and the inflection point for growth (t_i) occurred correspondingly earlier in the dunlin (*t*-test: $t_{52} = -13.7$, $P < 0.0001$; fig. 4.1; table 4.1). The pectoral muscles of both species were relatively small at hatching, and as with body mass, the growth constant of the dunlin was more than 100% higher than that of the whimbrel. At 16 d of age, pectoral muscles in both species were still growing rapidly. The growth constant of the leg was 50% higher in the whimbrel than in the dunlin. Compared to the pectoral muscles, growth was rapid, and at 16 d of age, the leg muscles had already reached adult size (fig. 4.1; table 4.1).

The size of the pectoral muscle as a proportion of body mass started out low and at a similar value for both species (fig. 4.2). In the dunlin, this value increased rapidly over the next 16 d, whereas in the whimbrel it remained low. The size of the leg muscle as a proportion of body mass started out higher than that of the pectoral muscle and changed little over the first 16 d of age. The two species showed a similar pattern in development of proportional leg muscle size. In adult birds, pectoral muscles were similar proportions of body mass in both species, but the leg muscles of adult whimbrels were smaller compared with those of adult dunlins, in contrast with the relative sizes of the leg muscles in the chicks.

Table 4.1. Asymptotic size (A), growth constant (K), inflection point (t_i), coefficient of determination (r^2), and sample size (n) for dunlin and whimbrel chicks. Standard errors given in parentheses. Growth parameters were determined by Gompertz curve fitting. For details, see Material and methods.

	A (g)	K	t_i (d)	r^2	n
body mass:					
dunlin	50	0.123 (0.006)	6.68 (0.387)	0 .927	24
whimbrel	380	0.075 (0.002)	13.71 (0.338)	0 .963	30
leg muscle mass:					
dunlin	2.6	0.200 (0.025)	4.37 (0.368)	0 .953	12
whimbrel	10.1	0.312 (0.079)	2.93 (0.422)	0.895	12
pectoral muscle mass:					
dunlin	9.6	0.104 (0.010)	15.42 (1.230)	0 .952	12
whimbrel	71.5	0.047 (0.006)	36.35 (3.805)	0 .896	12

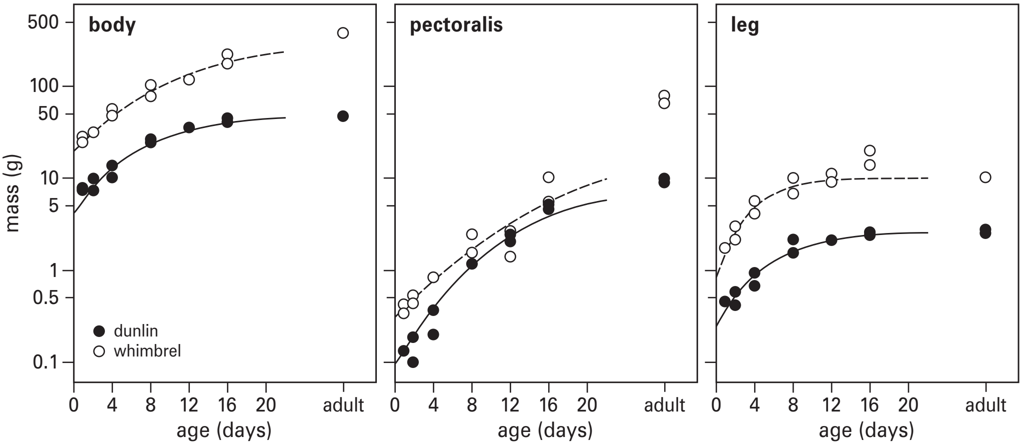

Figure 4.1. Body mass, leg muscle mass, and pectoral muscle mass in chicks of dunlin and whimbrel shown as a function of age. The lines denote the average growth curves obtained by nonlinear curve fitting of the Gompertz equation.

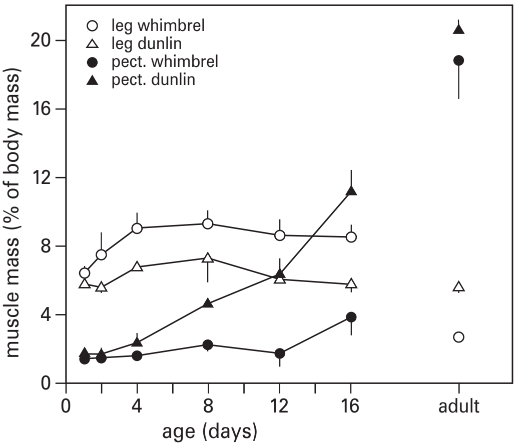

Figure 4.2. Muscle mass as percentage of body mass with standard deviations in relation to age, for the leg and pectoral muscles of dunlin and whimbrel chicks and adults.

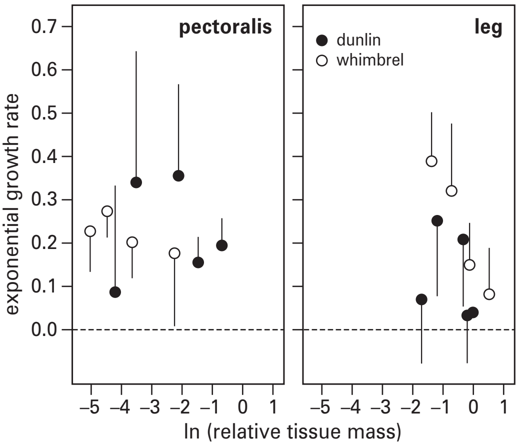

Figure 4.3. Relationship between the exponential growth rate and the natural logarithm of relative tissue mass (calculated as ln [tissue mass/ adult tissue mass]), for pectoral and leg muscles of dunlin and whimbrel, with standard errors. Only growth increments up to 16 d of age were used.

The relative growth rates obtained from fitting Gompertz equations are reflected in the EGR. As shown in figure 4.3, EGRs of the pectoral muscle were generally higher in the dunlin than in the whimbrel. After an initial low value, the EGR of the dunlin increased rapidly to a higher level than that of the whimbrel and remained relatively high almost until adult mass was achieved. EGRs of leg muscle were higher in the whimbrel early in the growth period.

Using a criterion of nonoverlapping asymptotic standard errors, statistically significant differences in growth rate are summarized as follows: WHleg ≥ DNleg > DNpect > WHpect. The growth rate for whimbrel leg muscle may be inflated because muscle mass exceeded the adult level during the growth period and because adult mass was used to estimate the Gompertz growth rate.

Development of catabolic enzyme activity

The developmental course of muscle mass-specific enzyme activity is shown in figure 4.4. For all tissues and enzymes, adult levels were similar in the whimbrel and dunlin, and enzyme activities were higher in pectoral than in leg muscle.

The most striking aspects of the development of CS activity were its relatively high level in the leg muscles compared to the pectoral muscles of young chicks and its more rapid development toward adult levels in the dunlin compared to the whimbrel. CS activity of pectoral muscles was lower in whimbrel compared to dunlin chicks at all ages (ANOVA with species and age: DNpect > WHpect, $F_{2,21} = 38.5$, $P < 0.0001$). CS activity of leg muscles also was lower in whimbrel at all ages except 16 d (ANOVA with species and age: DNleg > WHleg, $F_{2,21} = 11.9$, $P < 0.0001$). A single statistical model for chicks showed that differences in CS activity could be attributed to species, tissue type, age, and the three-way interaction between these factors (GLM, age as random factor: intercept $F_{1,5} = 47.9$, $P < 0.001$; species $F_{1,16} = 19.9$, $P < 0.0005$; tissue type $F_{1,16} = 9.6$, $P < 0.01$; age $F_{5,16} = 4.7$, $P < 0.01$; species × tissue type × age $F_{16,24} = 6.2$, $P < 0.0005$).

HOAD activity showed complex patterns of development (fig. 4.4). HOAD activity was higher in the leg than in the pectoral muscles in both species, but this was not significant in the dunlin due to the high activity level measured in the pectoral muscle at day 8 (ANOVA with tissue type and age: WHleg > WHpect, $F_{2,21} = 13.0$, $P < 0.0001$). As with CS, HOAD activity was initially higher in the leg muscles than in the pectoral muscles. Combining these effects in a single statistical model showed that differences in HOAD activity in the chicks could be attributed to tissue type, age, and the interaction between species, tissue type, and age (GLM, age as random factor: intercept $F_{1,5} = 74.8$, $P < 0.0005$; tissue type $F_{1,17} = 6.3$, $P < 0.05$;

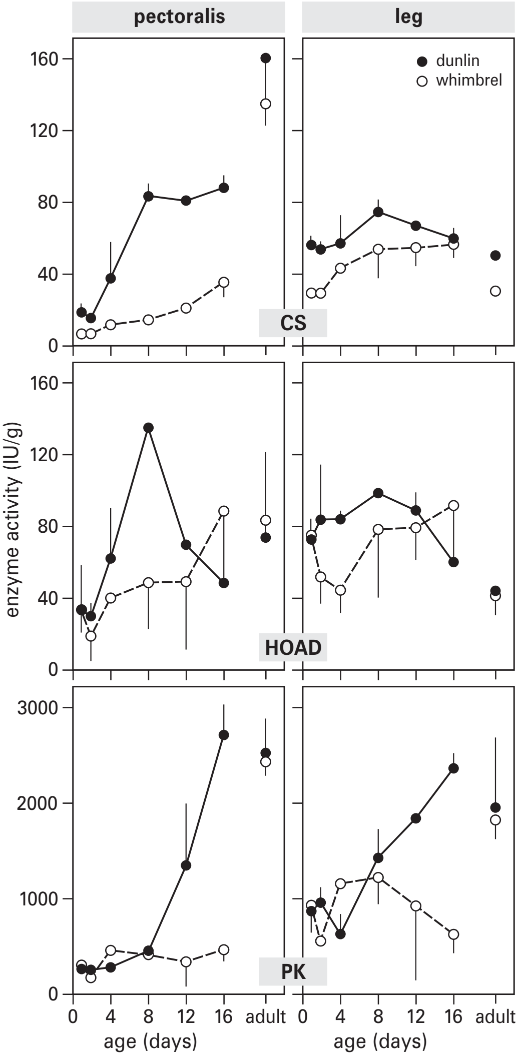

Figure 4.4. Activity of citrate synthase (CS), l-3-hydroxyacyl-CoA-dehydrogenase (HOAD) and pyruvate kinase (PK) with standard deviations of leg and pectoral muscles in dunlin and whimbrel chicks (and adults), in relation to age.

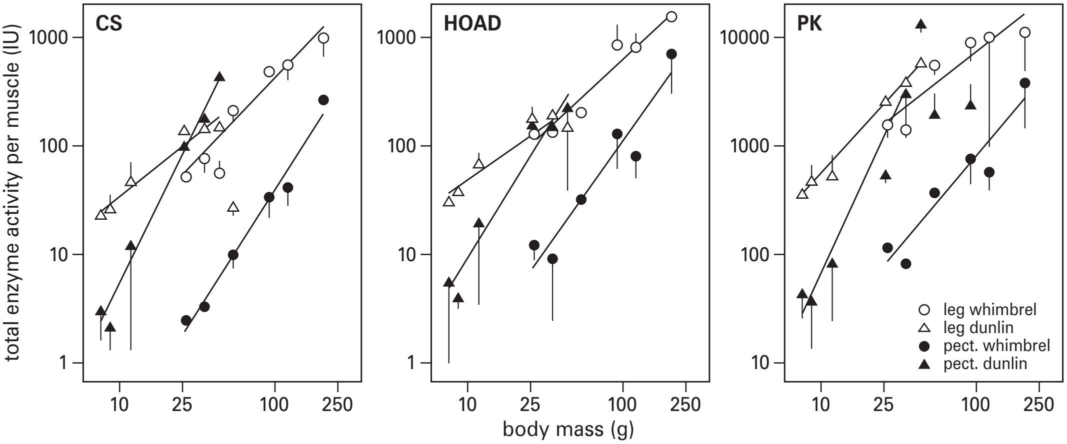

Figure 4.5. Total activity (enzyme activity multiplied by muscle mass) of citrate synthase (CS), l-3-hydroxyacyl-CoA-dehydrogenase (HOAD), and pyruvate kinase (PK), with standard deviations in relation to body mass for leg and pectoral muscles of dunlin and whimbrel chicks. The lines depict linear regressions.

age $F_{1,\,17} = 3.3$, $P < 0.05$; species × tissue type × age $F_{17,\,24} = 2.34$, $P < 0.05$). Differences between species were not significant.

As with CS and HOAD, PK activity was higher in the leg muscles than in the pectoral muscles of both species until 16 d of age (fig. 4.4; ANOVA with tissue type and age: DNleg > DNpect, $F_{2,\,21} = 43.8$, $P < 0.0001$; WHleg > WHpect, $F_{1,\,22} = 25.1$, $P < 0.0001$; age not significant). PK activity of dunlin pectoral and leg muscles increased rapidly until day 16 to levels similar to those of adults. PK activity in the whimbrel remained relatively low and constant compared to the dunlin until 16 d of age, after which it increased fivefold (pectoral muscles) or threefold (leg muscles) to adult levels. A single statistical model showed that PK activity was related to tissue type, the interaction between species and age, and the interaction between tissue type and age (GLM, age as random factor: intercept $F_{1,\,6.8} = 19.3$, $P < 0.005$; tissue type $F_{1,\,5} = 15.4$, $P < 0.05$; species × age $F_{6,\,30} = 28.6$, $P < 0.0005$; tissue type × age $F_{5,\,30} = 3.2$, $P < 0.05$).

Total activity of the pectoral and leg muscle

Multiplying the enzyme activity per unit mass by the mass of the muscle gives the total enzyme activity of the individual muscle (fig. 4.5) and provides an estimate of the potential contribution of the muscle to the heat balance of the chick (see Choi *et al.* 1993). This estimate is more strongly influenced by variation in muscle mass than in mass-specific enzyme activity. In both species, leg muscle contributed most of the potential total enzyme activity early in development, although pectoral muscles predominated after 12 d in the dunlin and sometime after 16 d in the whimbrel. Total enzyme activities for leg muscle in the dunlin and whimbrel had similar allometric relationships. For pectoral muscles of the same weight, however, dunlin chicks consistently exhibited higher catabolic capacity.

Growth rate versus functional capacity

The hypothesis that there is a trade-off between exponential growth rate and functional capacity predicts that the correlation between the two should be negative. This prediction is generally borne out by the data, especially for the leg muscles (fig. 4.6). Since the sample size of age

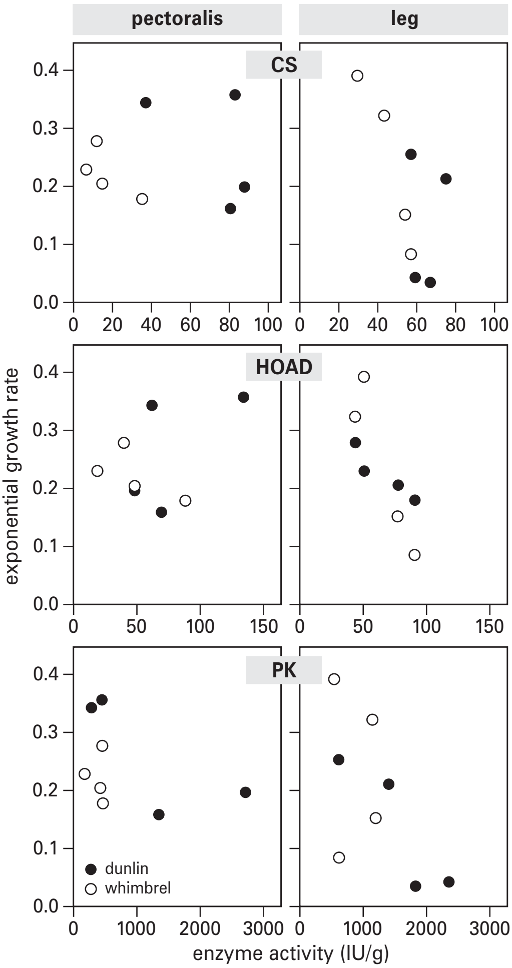

Figure 4.6. Exponential growth rate in relation to the activity of citrate synthase (CS), l-3-hydroxyacyl-CoA-dehydrogenase (HOAD), and pyruvate kinase (PK) for pectoral and leg muscles of dunlin and whimbrel .

increments was small, these results allow us to form only a general concept of the relationship between enzyme activity and EGR. Statistics combining the data for the pectoral and the leg muscle in one model revealed that for both CS and PK the correlation between enzyme activity and EGR was significantly negative (GLM: CS: $F_{4,\,11} = 10.9$, $P < 0.001$, $r^2 = 0.80$; CS activity $F_{1,\,11} = 35.2$, $P < 0.0001$; species, tissue type, and the interaction between tissue type and CS activity all contributed significantly to the model; PK: $F_{4,\,14} = 8.0$, $P < 0.05$, $r^2 = 0.37$; significant contribution of PK activity only). EGR showed no significant correlation with HOAD, although there appeared to be a negative relationship in the leg muscles.

Discussion

Growth

Growth rate was higher in the smaller dunlin than in the whimbrel (fig. 4.1, table 4.1). These values corresponded well with growth rates calculated from other data on hand-reared chicks of these species (Visser & Ricklefs 1993a), and they are in line with the general inverse relationship of relative growth rate to body size (e.g., Ricklefs 1968; Starck & Ricklefs 1998). Muscle growth rate was higher in the leg than in the pectoral muscles in both dunlin and whimbrel (fig. 4.1) and showed the importance of rapid development of the leg, which is needed for locomotion and early thermoregulation. This is also reflected in the high relative mass of the leg muscles (proportional to body mass) compared to the relative mass of the pectoral muscles in both species (fig. 4.2). Pectoral muscles, in contrast, are small in young precocial chicks and are not able to contribute substantially to heat generation until the chicks are older and start to fly. Until this time, growth and functional development are delayed in these muscles (Barré *et al.* 1985; Dietz *et al.* 1997; Marjoniemi & Hohtola 1999). Accordingly, the absolute as well as the relative size of the pectoral muscles was low initially but increased to a size exceeding that of the leg muscles later in development. This happened sooner in the dunlin than in the whimbrel because growth was more rapid in the pectoral muscles of the dunlin than the whimbrel. This correlates with earlier development of flight in the dunlin (del Hoyo *et al.* 1996).

Development of catabolic capacity

Among adults, the catabolic profiles of the muscles were similar for the two species. The activities of all three enzymes were higher in the pectoral than in the leg muscles. In the chicks, enzyme activities in the leg muscles tended to be higher than in the pectoral muscles, at least early in development, and were close to or exceeded adult levels of enzyme activity in the leg muscles. The leg muscles are needed for locomotion shortly after hatching. Clearly, they also make up the bulk of the thermoregulatory capacity of the chick early in development. Enzyme activity in the pectoral muscles increased at later ages than in the leg muscles, although generally to higher levels. Since the dunlin grew more rapidly than the whimbrel, enzyme activities of dunlin chicks attained adult levels earlier, in some cases by 16 d of age, than did those of whimbrel chicks. Dunlin chicks also tended to have higher levels of enzyme activities than whimbrel chicks at any given age.

When we include the size of the muscles and consider the total enzyme activity (enzyme activity multiplied by the muscle mass), it becomes clear that the leg muscles of whimbrel and dunlin chicks had similar capacities relative to body mass, whereas the pectoral muscles of the dunlin had a higher capacity than those of the whimbrel. This indicates that whereas dunlin chicks rely more on catabolic capacity to generate heat, whimbrel chicks, to a considerable extent, can rely on the thermal inertia of their larger mass to reduce heat loss. This may explain why the whimbrel chick is homeothermic at only 3 d of age, whereas the dunlin does not achieve homeothermy until 8 d of age (Visser 1991).

Compared to altricial chicks, precocial chicks exhibit slow growth but have a high level of function. Enzyme activities can now be compared over a range of altricial species (bank swallow R*iparia riparia*, Marsh & Wickler 1982; red-winged blackbird *Agelaius phoeniceus*, Olson 1990; European starling *Sturnus vulgaris*, Choi *et al.* 1993) and precocial species (Japanese quail *Coturnix coturnix japonica*, Choi *et al.* 1993 and Shea *et al.* 1995; northern bobwhite *Colinus virginianus*, Choi *et al.* 1993; barnacle goose *Branta leucopsis*, Bishop *et al.* 1995; dunlin and whimbrel, this study). These studies reveal that the aerobic capacity (CS) of pectoral muscles increases rapidly after hatching in altricial chicks and is generally higher than in precocial chicks. CS activities of leg muscles were similar in the two groups. Glycolytic capacity (PK) was much higher in precocial species from hatching on. Starlings exhibited the lowest glycolytic capacities, Japanese and bobwhite quail were intermediate, and dunlin and whimbrel had the highest capacities. This indicates that, besides aerobic catabolism, glycolytic catabolism plays an important role in ATP production and, therefore, presumably in heat production in chicks of precocial shorebird species, evidently more so than in chicks of altricial species. Shorebird chicks also have a relatively high capacity to break down fatty acids. For example, the levels of HOAD activity in the leg muscles are more than 10 times higher than in the chicks of the red-winged blackbird; in pectoral muscles, HOAD activities of shorebird chicks are about three times higher than those of red-winged blackbird chicks.

Both glycolysis and β-oxidation produce acetyl CoA, which would be available to the mitochondria as substrate for the TCA cycle. The ontogenetic changes in capacities observed here suggest that ß-oxidation may be relatively more important as a source of acetyl CoA earlier in development than it is later. In pectoral muscle, for example, the large increase in HOAD activity in the dunlin at day 8, followed by the striking decrease in HOAD activity and simultaneous increase in PK activity after day 8, suggests a qualitative shift in the importance of these two pathways during development.

Catabolic capacity as a measure of mature function

To assess the suitability of catabolic enzyme activity as an estimate of functional maturity, we

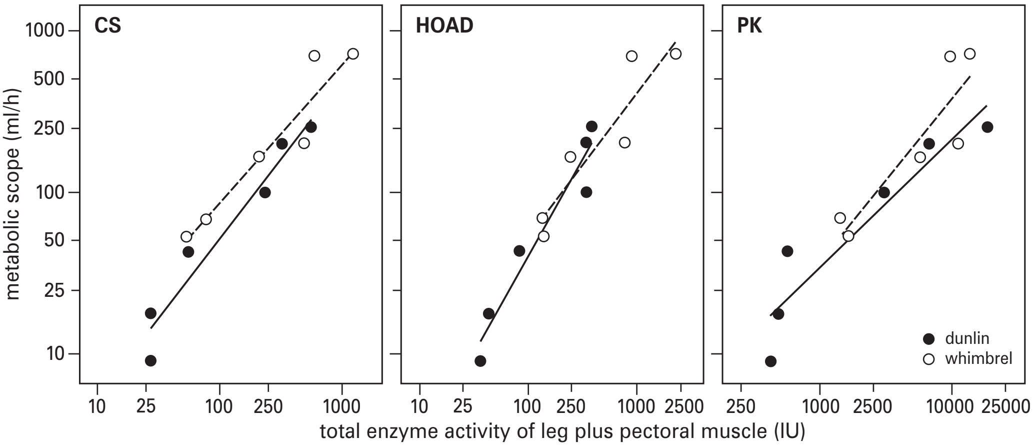

Figure 4.7. The relationship between metabolic scope and total enzyme activity summed for pectoral and leg muscle, plotted for citrate synthase (CS), l-3-hydroxyacyl-CoA-dehydrogenase (HOAD), and pyruvate kinase (PK) of dunlin and whimbrel chicks. The lines depict linear regressions..

correlated total enzyme activities with the metabolic scope of shorebird chicks measured in a parallel study (JB Williams *et al.*, unpublished data). Briefly, standard (SMR) and peak metabolic rates (PMR) of dunlin and whimbrel chicks were measured using an opencircuit respirometer. Temperature was initially maintained within the thermoneutral zone to obtain an estimate of SMR and then was decreased by about 0.5°C min^{-1} until metabolism reached PMR and subsequently began to decrease. Body temperature was monitored continuously throughout the trials. Metabolic scope was calculated as PMR–SMR. Metabolic measurements were obtained from chicks of similar age and body mass as those for which we measured enzyme activities.

The metabolic scope of dunlin and whimbrel chicks was significantly correlated with the total enzyme activity of the muscles (*i.e.*, activity multiplied by muscle mass) for all three enzymes (fig. 4.7), suggesting that the total catabolic capacity of the pectoral and leg muscles is a good predictor of heat generation in the chick (see also Choi *et al.* 1993; GLM: ln[metabolic scope] vs. ln[total enzyme activity]; CS: slope = 0.99, $F_{1,\,10} = 106.1$, $P < 0.0001$, $r^2 = 0.91$; HOAD: slope = 1.04, $F_{1,\,10} = 106.9$, $P < 0.0001$, $r^2 = 0.91$; PK: slope = 0.90, $F_{1,\,10} = 60.2$, $P < 0.0001$, $r^2 = 0.86$). However, this correlation was explained by variation in the mass of the muscles and not in enzyme activity itself. A statistical model with muscle mass and mass-specific enzyme activity as separate effects showed that enzyme activity was not significant (GLM: metabolic scope vs. mass of leg+pect and CS activity g^{-1} of leg + pect; all log transformed: $F_{2,\,9} = 19.9$, $P < 0.0001$, $r^2 = 0.82$; effect of muscle mass $P < 0.0001$ effect of CS activity $P < 0.05$; similar correlations were found for HOAD and PK). Why enzyme activity itself did not have an effect on metabolic scope can be explained partly by the fact that enzyme activity in the leg muscles changed relatively little during early development. Thus, the rapidly increasing mass of the leg muscle alone had an important effect on metabolic scope. In addition, the pathways that are used by the chicks to generate ATP change throughout development, as indicated by the ontogenetic changes in the relative activities of the three enzymes. Accordingly, levels of CS, PK, and HOAD activity not only increase with age but may also decrease as the need for a certain pathway diminishes. Because of this, the relationship between enzyme activity per gram tissue and metabolic scope and functional maturity is weakened, and thus, enzyme activity might not be a totally consistent indicator of muscle maturity.

Trade-off between growth rate and functional maturity

Exponential growth rate was negatively correlated with CS activity per gram tissue (fig. 4.6), which matches our expectations regarding a trade-off between growth rate and functional maturity. However, differences in levels of enzyme activities between the two species and between the leg and pectoral muscles indicate that processes other than this trade-off play important roles in determining catabolic capacity and growth rate. For example, dunlin chicks both grew more quickly and demonstrated relatively higher catabolic capacities than whimbrel chicks (figs. 4.1, 4.3–5). Analyses using individual muscle groups lead to a similar conclusion. For example, the catabolic capacities in the leg muscles were initially higher than in the pectoral muscles even though growth rate of the leg muscles was higher than that of the pectoral muscles (figs. 4.1, 4.4). These results can be related partly to qualitative differences in the catabolic capacities of the tissues, and they stress the importance of further studies on structural and functional properties of tissues. The results may also be explained simply by the heat-regulating effect of the mass of the chicks. The smaller dunlin chicks seem to rely more on the catabolic capacity of their muscles and invest more energy in rapid development of both pectoral and leg muscles than do the whimbrel chicks. The larger mass of the whimbrel chick apparently reduces the need for rapid functional maturation of the muscles. As the leg muscles of the whimbrel chick are crucial for locomotion and heat generation, a considerable amount of energy is invested in their rapid growth, but catabolic capacity is nonetheless relatively low compared to the dunlin. The pectoral muscles of the whimbrel chick both grow more slowly and have a lower enzyme activity than the pectoral muscles of the dunlin chick. As whimbrel chicks develop flight later than dunlin chicks (del Hoyo *et al.* 1996), development of the flight apparatus can be delayed, while resources are focused on, for example, the legs, skeleton, feathers, or the brain (Portman 1962; Carrier & Auriemma 1992).

The data presented in this article suggest that catabolic capacity together with body mass determine the functional output of the shorebird chick. A small chick needs to invest in both growth and mature function to its maximum capacity in order to stay warm during foraging. Because of its larger size, a larger chick is able to maintain its body temperature to a large extent. A high level of functional maturity seems to be less important in a larger chick, and consequentially, it may reduce its daily energy demand by lowering its level of functional maturity.

Acknowledgements

We kindly thank the Churchill Northern Studies Centre for their logistic support and housing. JB Williams provided unpublished data on whole-body metabolism in growing dunlin and whimbrel chicks. GH Visser supported the study throughout and made useful comments to the manuscript, as did S Daan and JM Starck. We thank J Spina, A Smeglin, M Hafey, and H Simoes for assisting us with the assays and data entry. This study was supported by National Science Foundation grant OPP-9453522 awarded to RER and GH Visser.

Chapter 5

Daily energy expenditure in precocial shorebird chicks: smaller species perform at higher levels

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Abstract

We measured daily energy expenditure (DEE) during the development periods of precocial chicks of five species of arctic shorebirds spanning a broad range in size, in order to investigate the relationships between DEE, body size and growth rate. We also quantified the effect of weather conditions on the energy expenditure of chicks to establish the impact of cold arctic weather on their time and energy budgets. We used the doubly labelled water method to measure DEE at ambient temperatures in an outside enclosure on the sub-arctic tundra at Churchill, Manitoba, Canada.

Growth rate was highest in the smallest species, and in general decreased with adult size, as shown by the decrease in growth rate constant and later inflection point with increasing adult body mass.

DEE ranged from 14 kJ day^{-1} in young chicks of the smaller species to 365 kJ day^{-1} in older chicks of the larger species. From hatching onward, DEE of shorebirds was high compared to DEE of chicks of altricial species, reflecting the high costs for locomotion and thermoregulation, and mass-specific DEE increased rapidly to adult levels.

Chicks of smaller species metabolized more energy per unit mass and functioned at higher multiples of resting metabolic rate than chicks of larger species. As chicks of smaller species also had higher growth rates, and thus simultaneously invested in growth and mature function, shorebird chicks apparently can adjust total metabolizable energy as well as its relative allocation between investment in growth and mature function.

DEE was similar to cold-induced peak metabolic rates achieved by shivering thermogenesis. Because chicks were motionless during laboratory metabolism measurements, the relatively high level of DEE compared to these metabolic rates suggests that locomotion produces similar amounts of heat as shivering.

Ambient temperature did not affect DEE in outdoor pens, although higher wind speed resulted in slightly increased energy expenditure. Heat produced by locomotion is possibly sufficient to sustain thermoregulation under local environments. Furthermore, when ambient temperatures are low, chicks spend more time brooding and less time foraging, which presumably counters the tendency to increase thermogenesis in response to cold.

Introduction

The harsh environment of the arctic imposes critical limits to the existence of many species. One type of limit includes extreme physical conditions of the environment, such as low temperatures and high wind velocities (Bakken *et al.* 2002). Another is the brevity of the growing season (MacLean & Pitelka 1971, Nettleship 1973). The arctic is a demanding environment for sandpipers (Scolopacidae) during the two- to three-month breeding season. Sandpiper chicks are self-feeding and in some species weigh as little as four grams at hatching, which places them among the smallest of endothermic animals. The precocial mode of development of sandpiper chicks presumably requires a high level of energy expenditure for locomotion and thermoregulation, particularly in the cold environments at high latitudes (e.g., West & Norton 1975; Starck & Ricklefs 1998, Schekkerman & Visser 2001, Schekkerman *et al.* 2003). Combined with pressure to grow rapidly during the short period of favourable conditions, shorebird chicks might operate near the limits of metabolic performance. However, few studies have measured the daily energy expenditure (DEE) of precocial chicks of any species under free-living conditions, hence little is known about the effects of biotic and abiotic factors on the DEE of sandpiper chicks (e.g., Drent *et al.* 1992).

Schekkerman & Visser (2001) showed that levels of daily metabolized energy of chicks of black-tailed godwits (*Limosa limosa*) and northern lapwings (*Vanellus vanellus*) in temperate grassland habitats in the Netherlands were about 60% higher than levels predicted for altricial chicks of similar size (Weathers 1992), for which food and heat are supplied by the parents. However, shorebirds in the Netherlands experience mild physical environments compared to those in many areas of the arctic. Consistent with this difference, rates of energy metabolism in arctic red knot chicks (*Calidris canutus*, Schekkerman *et al.* 2003) were higher than those of godwits and lapwings in the Netherlands.

Young precocial chicks, particularly those of small species that experience low environmental temperatures, lose heat rapidly during foraging (Chappell 1980, Visser & Ricklefs 1993b, Krijgsveld *et al.* 2003a [chapter 7]). When not actively foraging, they respond to cooling by shivering to generate heat (Dawson 1975, Hohtola & Stevens 1986), but often neither mechanism can produce enough heat to prevent body cooling (Ricklefs & Williams 2003). Therefore, foraging is regularly interrupted by periods of brooding by the parent, during which body temperature is restored to higher levels. The better a chick can maintain its body temperature, the more time can potentially be spent foraging. This capacity to produce heat, and therewith to maintain body temperature, is primarily the product of the mass of a chick's skeletal muscle and its maximum tissue-specific metabolic rate. Thus, the capacity of the chick to generate heat increases over the growth period as size and maturity (% of adult function) of the skeletal muscles increase (Ricklefs 1983, Choi *et al.* 1993, Krijgsveld *et al.* 2001 [chapter 4]). In this respect, body size plays an important role in the level of energy expenditure of the chick, because smaller chicks have higher mass-specific thermal conductance (Visser & Ricklefs 1993a,b; Bakken *et al.* 2002).

When they are cold-stressed, chicks of small shorebird species generally increase their metabolism proportionately more than do large species (Kendeigh 1969; Williams *et al.* 2007). Krijgsveld *et al.* (2001; chapter 4), by measuring enzyme activity in the flight and leg muscles, found that in two species of shorebird chicks, the skeletal muscles of the smaller species (dunlin *Calidris alpina*) had a higher functional capacity than those of the larger species (whimbrel *Numenius phaeopus*), enabling them to increase their metabolic rate proportionately more. These results suggest that chicks of smaller species should exhibit proportionately higher mass-specific DEE in response to cold stress than chicks of larger species.

To test this, we measured DEE in outdoor enclosures, using the doubly labelled water method, throughout the growth periods of the chicks of five species of sandpipers ranging in neonatal mass from 4 to 33 g. From the smallest, the species were least sandpiper (*Calidris minutilla*), dunlin, lesser yellowlegs (*Tringa flavipes*), Hudsonian godwit (*Limosa haemastica*), and whimbrel. We also determined the effect of ambient temperature on DEE, and we related DEE to resting and peak metabolic rates as measured by Williams *et al.* (2007) under laboratory conditions.

Methods

Birds and housing

DEE was measured in chicks of least sandpiper (n = 5), dunlin (n = 7), lesser yellowlegs (n = 6), Hudsonian godwit (n = 12; repeated measurements after 12 and 24 h in 2 chicks) and whimbrel (n = 15), at ages ranging from 2 to 17 days (hatch day = 0). Eggs were collected on the tundra near Churchill (58°45'N, 94°04'W), Manitoba, Canada, in June and July during fieldwork in 1995 through 1998. Eggs were incubated at an air temperature of 37°C and a relative humidity of 55%, which was increased to 80–90% at the first signs of hatching (starred eggshell), ca. two days before hatching. Chicks were kept for a minimum of one day in boxes in the laboratory to allow them to dry and start feeding. Heat was supplied by a light bulb, creating a range of temperatures in the box, and food and water were supplied *ad libitum*. For a detailed description of housing conditions, see Krijgsveld *et al.* (2001; chapter 4).

In 1995 through 1997, each chick was placed in an outside enclosure for the duration of its doubly labelled water measurement. On non-experimental days chicks were held outdoors for 4–6 hours every day to every other day, throughout their growth period from 1–2 days after hatching. Otherwise chicks were kept indoors. In 1998, five whimbrel chicks in which DEE was measured additionally were held outdoors continuously from one day after hatching. Growth of chicks did not differ between years or deviate from growth of a group held continuously indoors. Growth curves under natural conditions are unfortunately not available, but data on growth of free-living and artificially-raised golden plover chicks in Churchill show that growth did not differ systematically between the two groups (KLK, unpublished data). DEE or ambient temperature during DEE-measurements did not differ consistently between 1998 and previous years.

Two types of enclosure were used, a small one for least sandpiper, dunlin, and lesser yellowlegs chicks up to ca. 10 days of age, and a larger one for all other chicks. The small enclosure was made of fine mesh (1 cm^2) hardware cloth, 50 cm high and 2 m square, covered by a lid of hardware cloth. The large enclosure was circular with a diameter of 15–20 m, consisting of 50 cm high chicken wire, lined along the lower 20 cm with cloth sealed to the ground. A cover protected chicks from predators. A heat source creating a thermal environment of up to 41°C was provided by a light bulb and a thermal blanket fitted in a wooden box (20 (h) × 30 (d) × 20 (w) cm), with an entrance of 15×15 cm. The light also served to direct the chicks to the brooder. Most chicks learned to use this brooder within a couple of hours and all chicks entered the brooder by the second day.

Because naturally available food diminished rapidly in the enclosure, food and water were supplied daily. Food was scattered on the ground to stimulate the chicks to forage. Food consisted of pheasant starter type 2 mix (1995 and 1996; Spelderholt, Beekbergen, Netherlands) or turkey pre-starter mix (1997 and 1998; Puratone Corporation, Niverville, MB, Canada), supplemented with a mix of tuna, chicken, oatmeal, and boiled eggs, as well as with dead mosquitoes.

Collecting of eggs was carried out under permit from the Canadian Wildlife Service. Husbandry and laboratory procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri–St. Louis, USA and the Canadian Wildlife Service.

Growth

Growth parameters were determined by fitting logistic growth functions to individual growth data using the nonlinear regression (NLR) procedure of SPSS Statistics release 12 (IBM Company). Because growth was not followed long enough to obtain a good estimate of the asymptotic mass of each individual chick, we set the asymptote to the average weights of adults taken during the breeding season in Canada and Alaska (least sandpiper - Johnsgard 1981; dunlin - Jehl & Murray 1986; lesser yellowlegs - Irving 1960; Hudsonian godwit - Jehl & Smith 1970; whimbrel - Dunning 1993).

Energy expenditure experiments

DEE was measured using the doubly labelled water method (DLW; Lifson & McClintock 1966, Nagy 1980, Speakman 1997). $^2H/^1H$ and $^{18}O/^{16}O$ ratios in blood samples were analyzed following procedures described in Visser & Schekkerman (1999). These authors validated the DLW method for growing shorebird chicks during 24 h-trials and showed that the relative error of DEE estimates was unrelated to the relative growth rate of the chick. For each DLW measurement in the present study, a chick was weighed and injected intraperitoneally with

0.0075 ml DLW g^{-1} in chicks of least sandpiper, dunlin and lesser yellowlegs and a linearly decreasing dosage of 0.0060 ml g^{-1} at 25 g to 0.0030 ml g^{-1} at 300 g body mass in chicks of Hudsonian godwit and whimbrel. In 1995 and 1996, the DLW mixture contained 30.0% ^2H_2O and 64.0% $H_2{}^{18}O$, in 1997 and 1998 it contained 33.8% ^2H_2O and 60.6% $H_2{}^{18}O$. After an equilibration period of 1 h, an initial blood sample was collected from the brachial vein in 4–6 glass capillary tubes each containing 10–15 μl of blood. Tubes were flame-sealed within 5 min.

After periods of 5 h 30 min to 28 h (intervals coinciding with simultaneous behavioural observations in a related study), during which the chick was in the enclosure, the chick was weighed again and the final blood sample was taken. In a total of 8 measurements on dunlin, Hudsonian godwit and whimbrel, the duration varied between 5 h 20 min and 6 h 10 min (mean = 5 h 55 min), in the other 37 chicks, duration varied between 10 h 30 min and 28 h (mean = 15 h 45 min; overall mean = 14 h, sd = 6.7). Neither interval length nor time during the diurnal cycle of activity affected DEE measurements.

Final labelled O_2-concentration as a percent of initial labelled O_2-concentration decreases as measurement duration increases. Final O_2-concentration averaged 83% after 6 h (sd = 2.6, n = 8), 61% after 12 h (sd = 11.3, n = 28), and 45% after 26 h (sd = 8.34, n = 11). Measurement duration did not affect smaller and larger species differently. Levels of DEE in the shorebird chicks were so high that a sufficient decrease in ^2H and ^{18}O could be obtained during even the short intervals. H:O ratio (fractional turnover rate of ^2H [deuterium, k_d] as percent of that of oxygen [k_o]) did not change with measurement duration for durations of less than 7 h versus more than 11 h, respectively, for dunlin: mean = 62.1% (sd = 6.13, n = 3) vs 61.2 (6.26, 4); Hudsonian godwit: 80.0 (3.13, 2) vs 80.1 (7.28, 12); whimbrel: 81.4 (4.21, 3) vs 82.4 (6.60, 12)).

To further evaluate the applicability of the DLW method during relatively short measurement periods (average = 12.0 h, sd = 0.62, n = 17 trials) a DLW validation experiment was conducted with chicks of dunlin (n = 8), American golden plover (*Pluvialis dominica* n = 3), Hudsonian godwit (n = 2), and lesser yellowlegs (n = 3). An initial blood sample (I) was taken after an equilibration period of one hour after injection, during which time the chick was fasting in a heated cardboard box. Next, the bird was placed in a respiration chamber and provided *ad lib* access to water and food of the same type as during normal housing, with lights on at all times. Ambient temperature was set between 25°C (for the heaviest chicks) and 35°C (smallest chicks), representing the lower limit of the thermoneutral zone. After a measurement period of 12 h, the bird was taken out of the chamber and a first final blood sample (F12) was collected as described above. In some cases, the chick was placed back in the respiration chamber for a second 12-h measurement period, at the end of which we collected a second final sample (F24). This provided a paired comparison with the first measurement period to address the issue of differential isotope incorporation. Respirometry measurements were carried out as described in Williams *et al.* (2007).

For these validation experiments, no significant relationship ($P = 0.44$) could be demonstrated between the error of the DLW method (relative to gas analysis) and the duration of the DLW sampling interval. The measurements revealed that with the application of Visser & Schekkerman's equation (1999), the error of the DLW method relative to the respirometry method, *i.e.* accuracy, was on average +1.3%, whereas the standard deviation (sd), *i.e.* precision, was 12.0% (GHV, unpublished data). The average error and sd for short measurements were close to those observed during the 24-h trials (0%, and 10.1% respectively; Visser & Schekkerman 1999). Thus, reducing the measurement period in this study did not affect the accuracy of DLW measurements and decreased the precision of estimates only slightly.

In two Hudsonian godwits we took final blood samples after both 12 and 24 h. DEE did not differ between the two interval lengths (after 12 and 24 h respectively: godwit #1, 17 days old: 365 and 365 kJ day^{-1}; godwit #2, 16 days old: 324 and 301 kJ day^{-1}).

In eight chicks, no initial blood sample was taken, but only a final blood sample (*i.e.*, single sample protocol, Ricklefs *et al.* 1986, Webster & Weathers 1989). Background isotope levels collected from five chicks (dunlin, whimbrel and free-living American golden plover [*Pluvialis dominica*, unpublished data Jan van Gils]) were similar to each other.

DLW analysis

$^2H/^1H$ and $^{18}O/^{16}O$ isotope ratios of the blood samples were determined at the Centre for Isotope Research, University of Groningen, Netherlands. Each blood sample was microdistilled using a vacuum line. ^2H was analyzed after conversion of the water sample to H_2 gas using a uranium oven at 800°C, and ^{18}O was analyzed using the CO_2-equilibrium method. In the H_2 and CO_2 gases, isotope ratios were determined with a dual inlet SIRA 9 isotope ratio mass spectrometer. Analyses were done in duplicate, but a third capillary of blood was analyzed if the two measurements differed by more than 2%. For details concerning the analytical procedure, see Visser & Schekkerman (1999).

Calculation of DEE from DLW measurements

Average background concentrations were 0.1996 atom percent for ^{18}O (sd = 0.00023, n = 5) and 0.0144 atom percent for ^2H (sd = 0.00008, n = 5). CO_2 production (rCO_2, liter per day) was calculated as:

$$rCO_2 = 22.4 \times [(N / 2.078) \times (k_o - k_d) - 0.13 \times 0.0249 \times N \times k_d]$$

where N represents the average size of the body water pool during the measurement (mol), and k_o and k_d the fractional turnover rates of the ^{18}O and ^2H isotopes, respectively. This equation was derived by Visser & Schekkerman (1999) from a validation study on shorebird chicks exhibiting a wide range of growth rates. In most chicks, the fractional turnover rates were calculated using the population-specific estimates for the background levels, and the individual-specific isotope concentrations of the initial and the final blood samples (equations 4 and 5 in Visser & Schekkerman 1999). When we obtained only a final blood sample, we estimated the initial concentration of each isotope using the injected dose and the size of the body water pool (see below, Webster & Weathers 1989).

To minimize the effect of errors in the quantity of DLW injected, N was not estimated from isotope dilution but from the relationship between percentage water content of the whole body and the fraction of adult mass attained by the chick (Visser & Schekkerman 1999, Schekkerman & Visser 2001). In all cases, N was calculated as the average of the estimated values at the start and end of the DLW measurement. Finally, DEE was calculated from rCO_2 using an energy equivalent of 27.33 kJ l^{-1} CO_2 which is in agreement with a protein-rich diet (Gessaman & Nagy 1988).

Environmental temperature

To relate DEE to thermal properties of the environment, we recorded environmental temperatures continuously throughout the season. A white and a black copper sphere, each having a diameter of 3.5 cm and containing a centrally positioned thermocouple, were placed 10 cm above the ground in a microhabitat characteristic of foraging shorebird chicks. The white sphere provided a measure of ambient air temperature (T_a), with the effects of wind and solar radiation largely factored out. The black sphere provided an approximation of the thermal environment with wind and solar radiation factored in, although not necessarily in the same fashion as experienced by the chick (Bakken *et al.* 1985, Walsberg & Weathers

1986). By subtracting white-sphere temperature from black-sphere temperature, we obtained a measure of radiative-convective load independent of T_a. These estimates matched levels obtained for comparison with a pyranometer (Anova: $F_{1,\ 117} = 623$, $P < 0.0001$, $r^2 = 0.84$; LI-200SA, Lincoln, NE, USA).

Wind speed was measured 10 cm above the ground with a cup anemometer (A100L2, Grant Instruments Ltd., Barrington, England; minimum threshold 0.15 m s^{-1}). In addition, data on wind speed at 10 m above ground, collected at the Churchill Airport, were provided by the Winnipeg Climate Centre (Winnipeg, Canada). Local climate data were averaged over 15-min intervals and recorded with a Squirrel 1204 data logger (Grant Instruments Ltd., Barrington, England).

Statistics

Variation in DEE with respect to species, age, and environmental conditions was analyzed with general linear models (GLM) unless specified otherwise, using SPSS Statistics release 12 (IBM Company). Mass, age, and environmental variables were entered as covariates, species as a fixed factor. For each separate analysis, the statistics for the individual covariates and factors are given, as well as the r^2 of the overall model.

Table 5.1. Comparison of masses and growth rates of five species of shorebirds. Neonatal (neon.) and adult body masses (g) are given, as well as the growth constant (K_L) and inflection point (t_i, days) determined by logistic curve fitting, and sample size used for determination of growth parameters (n individuals weighed daily).

species	body mass		K_L	t_i	n
	neon.	adult			
least sandpiper	4	21	0.240	7.7	26
dunlin	8	50	0.225	8.9	44
lesser yellowlegs	12	81	0.129	14.6	20
Hudsonian godwit	25	255	0.170	13.9	25
whimbrel	33	380	0.156	16.2	51

Results

Size

The smallest species, least sandpiper, grew the fastest, whereas the larger Hudsonian godwit and whimbrel grew more slowly (table 5.1). The growth rate constant (K_L) decreased and the inflection point increased with increasing adult body mass, following the general pattern of decreasing growth rate with increasing size, first described by Ricklefs (1973). In contrast, the chicks of lesser yellowlegs grew poorly compared to other studies on lesser yellowlegs (Visser & Ricklefs 1993a), and this resulted in a low growth rate constant and a late inflection point relative to their size. This did not affect the quality of the measurements of DEE (see Methods), although it may have contributed to the relatively low level of DEE in yellowlegs compared to the smaller dunlin. Chick growth (here proportional increase in mass) during DEE measurements was unrelated to ambient temperature.

DEE and time of day

DEE levels were lower when night-time hours (*i.e.* 22:30-3:30) comprised a larger proportion of the measurement period. This “night” effect could be accounted for by lower wind speeds at night (see below). After correction for wind speed, DEE did not show a significant variation with the fraction of the measurement that occurred during the night. This fraction was highest in chicks of least sandpiper and dunlin (both 24% versus 17% in the other species). Thus, DEE levels in these two species were likely somewhat underestimated compared to those of other species. Accordingly, we interpreted the results conservatively. Because we expected DEE to be higher in smaller species, this would not have biased our conclusions.

Daily energy expenditure

DEE ranged between 14 and 365 kJ day^{-1}. Values were lowest in chicks of least sandpiper and lesser yellowlegs, intermediate in chicks of

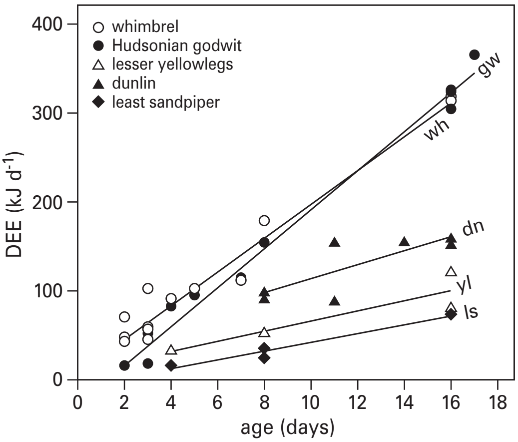

Figure 5.1. Daily energy expenditure as a function of age in chicks of five species of shorebirds covering a wide range of body size.

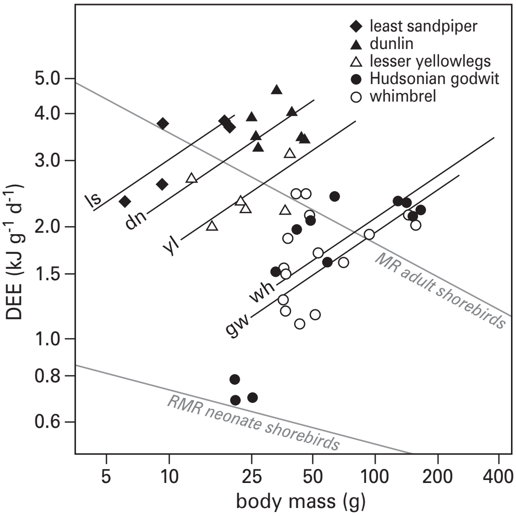

Figure 5.2. Daily energy expenditure per gram body mass as a function of body mass in chicks of five species of shorebirds representing a wide range in body size. Regression lines are plotted as solid lines, using the common slope for all five species (b = 0.38), and are extended to cover the full range in body mass from neonate to adult. Grey lines depict the resting metabolic rate of neonatal shorebird chicks (lower line; RMR = $0.020 \times \text{mass}^{-0.145}$ (kJ g^{-1} day^{-1}); Visser & Ricklefs 1993b) and the metabolic rate of adult shorebirds exposed to 10°C (upper line; MR = $912 \times \text{mass}^{-0.296}$ (kJ kg^{-1} day^{-1}); Kersten & Piersma 1987). Levels were higher in chicks of smaller than larger shorebird species, and were high from hatching onward, reflecting high costs for locomotion and thermoregulation.

dunlin, and highest in chicks of Hudsonian godwit and whimbrel (fig. 5.1). For unknown reasons, three young godwit chicks (2–3 days) had exceptionally low levels of DEE. Measurement intervals for these chicks were normal (14 h), and they showed a normal activity pattern (foraging 50% of the time, KLK unpublished data).

DEE of the shorebird chicks increased rapidly with age. Because chicks of the larger species weighed so much more at any given age than the smaller species, whole-body DEE was higher in the larger species. However, as a function of body mass, least sandpiper and dunlin had higher levels of DEE than godwit and whimbrel (GLM: log(DEE) significantly correlated with log(mass): $F_{1,\,39} = 389.4$, $P < 0.0001$; and with species: $F_{4,\,39} = 27.9$, $P < 0.0001$; $r^2_{\text{model}} = 0.925$; model excludes wind speed, see below). The rate of increase in DEE with body mass did not differ significantly between species (no interaction effect between log(mass) and species: $F_{4,\,35} = 1.60$, $P = 0.20$). The common scaling exponent of this regression was 1.38 ± 0.07 se; the intercepts were 0.10, -0.00, -0.13, -0.47 and -0.43, respectively, for least sandpiper, dunlin, lesser yellowlegs, Hudsonian godwit, and whimbrel (with [least sandpiper, dunlin] > [lesser yellowlegs] > [godwit, whimbrel]; based on LS means and significance of pairwise differences).

Because the exponent relating DEE to mass was greater than 1, mass-specific DEE also increased with body mass, except in the dunlin where the age range was probably too small to reveal an increase with mass (fig. 5.2). For a given body mass, mass-specific DEE generally was higher in chicks of smaller than of larger species (GLM; log(DEE g^{-1}) significantly corre-

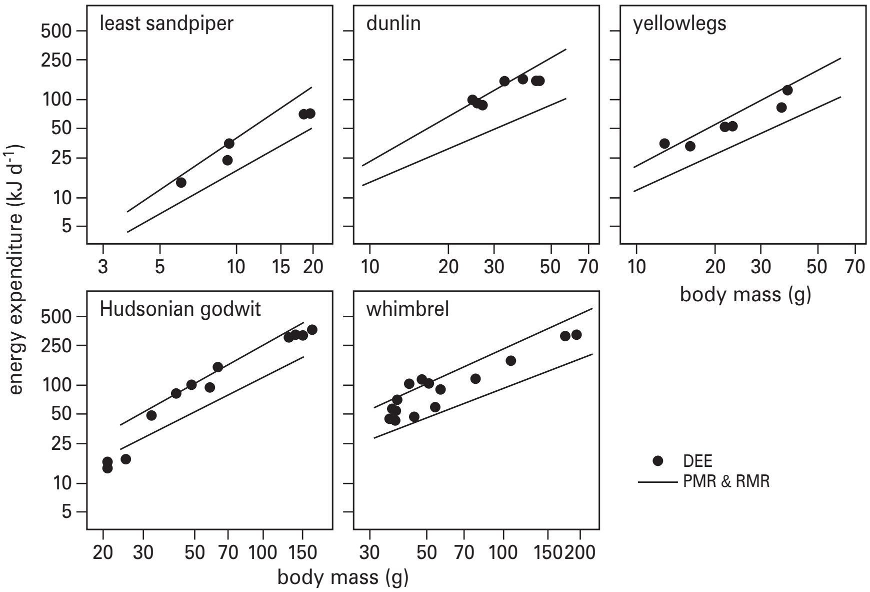

Figure 5.3. Daily energy expenditure (symbols) as a function of body mass, in relation to peak and resting metabolic rate (PMR and RMR, lines) in chicks of different species of shorebirds. PMR and RMR are shown as regression lines calculated from Williams *et al.* (2007).

lated with log(mass): $F_{1,36} = 33.6$, $P < 0.001$; and with species: $F_{4,36} = 33.1$, $P < 0.001$; $r^2_{\text{model}} = 0.79$, model including wind speed). Dunlin chicks showed the highest values of mass-specific DEE. Hudsonian godwit and whimbrel chicks had similarly low levels of mass-specific DEE. Since the within-species scaling exponent for whole-body metabolism was 1.38, mass-specific DEE increased with the 0.38 power of body mass (see McNab 1999, Hayes 2001).

Effect of ambient temperature and wind

Ambient temperature (T_a) in Churchill was high during the DEE measurements, averaging 20°C, with a minimum of 3°C and a maximum of 27°C. Average T_a was below 10°C for 5 out of 45 measurements, and it was between 10 and 20°C for 10 measurements. Although DEE increased slightly with decreasing T_a's, neither T_a nor radiative/convective load exerted significant effects on DEE.

Wind speed at chick height averaged 0.6 m s^{-1} during the measurements and reached a maximum of 2.9 m s^{-1}. Wind speeds just above ground were considerably lower than wind speeds measured at 10 m above ground, which averaged 4.4 m s^{-1} and reached a maximum of 10.8 m s^{-1}. Wind speed at ground level had a significant effect on DEE, but the increase in DEE with increasing winds was negligible (GLM: log(DEE) correlated significantly with wind speed 10 cm above ground; effect of minimum wind speed when added to the model: $F_{1,36} = 10.7$, $P < 0.01$, slope=0.3 log (DEE) units per m s^{-1}; r^2_{model} increases from 0.92 to 0.94. DEE was only correlated with wind speed at ground level, not at 10 m altitude).

DEE in relation to peak and resting metabolic rate

In most species, DEE was close to, or exceeded, peak metabolic rate (PMR) in response to cold stress measured in a flow-through respirometry

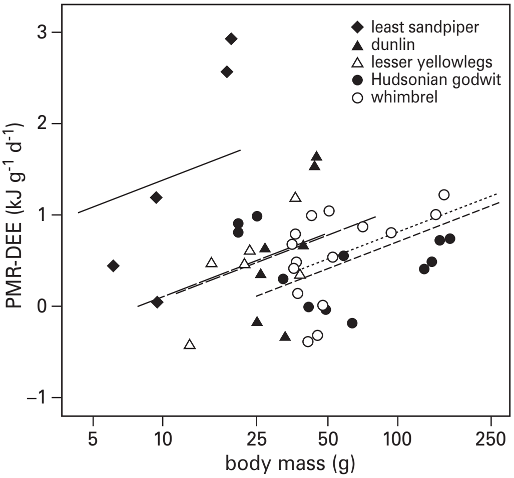

Figure 5.4. DEE in relation to PMR, in relation to body mass of chicks of different species of shorebirds. Values shown as mass-specific peak metabolic rate minus daily energy expenditure (PMR-DEE). Data on PMR from Williams *et al.* 2007. Regression lines are plotted using the common slope for all five species ($b = 0.98$), and are extended to cover the full range in body mass from neonate to fledging (increased hatching mass from smallest to largest species).

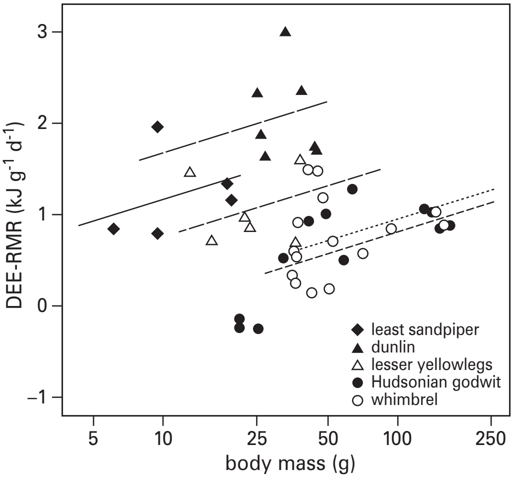

Figure 5.5. DEE in relation to RMR, in relation to body mass of chicks of different species of shorebirds. Values shown as daily energy expenditure minus resting metabolic rate (DEE-RMR). Data on RMR from Williams *et al.* 2007. Regression lines are plotted using the common slope for all five species ($b = 0.80$), and are extended to cover the full range in body mass from neonate to fledging (increased hatching mass from smallest to largest species).

system in the laboratory (fig. 5.3; Williams *et al.* 2007). DEE was closer to PMR when chicks were small than when they were larger, especially for least sandpiper chicks (fig. 5.4; GLM: difference significantly correlated with log (mass): $F_{1,39} = 6.3$, $P < 0.05$ and species: $F_{4,39} = 4.2$, $P < 0.01$; no interaction effect). Although the difference between PMR and DEE showed a larger increase with body mass in the smaller species than in the larger species, this difference was not significant, and therefore the common slope for all five species was plotted in fig. 5.4.

DEE was closely related to resting metabolic rate (RMR; linear regression DEE vs RMR (both in kJ g^{-1} day^{-1}): $F_{1,43} = 81.7$, $P < 0.001$, $r^2 = 0.66$). The elevation of DEE above RMR (DEE-RMR, kJ g^{-1} day^{-1}) increased with body mass within species, and was larger in the smaller species than in the larger species, with dunlin showing the highest level and Hudsonian godwit the lowest (fig. 5.5; GLM: mass-specific scope was significantly correlated with log (mass): $F_{1,39} = 7.8$, $P < 0.01$ and species: $F_{4,39} = 16.7$, $P < 0.001$; overall model $r^2 = 0.63$; no interaction effect).

Discussion

Rapid development of DEE

From hatching onwards, levels of DEE of all five species of shorebird chicks were high compared to those of altricial chicks (fig. 5.6). In altricial chicks, DEE was much lower than that of shorebird chicks of similar body mass, as in for example yellow-eyed junco (*Junco phaeonotus*, DEE = $0.456 \times \text{mass}^{1.656}$ (kJ/day, g), Weathers & Sullivan 1991) or savannah sparrow (*Passerculus sandwichensis*, DEE = $0.943 \times \text{mass}^{1.272}$ (kJ/day, g) Williams & Prints 1986). Neonatal

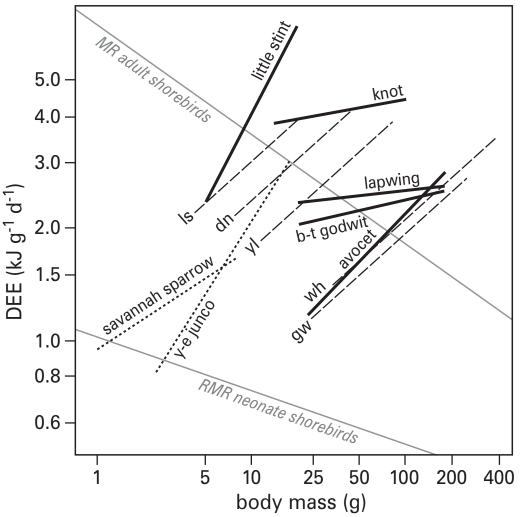

Figure 5.6. Comparison of mass-specific DEE between various altricial and precocial species, plotted as a function of body mass. As figure 5.2, with data of two altricial and five precocial species added from literature. Dashed lines – precocial species from this study (see fig. 5.2); filled lines – other precocial species; stippled lines – altricial species. Little stint – Tjörve *et al.* 2007; knot – Schekkerman *et al.* 2003; lapwing & black-tailed godwit – Schekkerman & Visser 2001; avocet – Joest 2003; savannah sparrow: Williams & Prints 1991; yellow-eyed junco: Weathers & Sullivan 1991. For additional information see text.

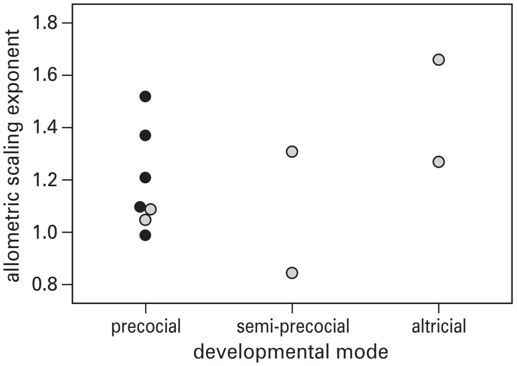

Figure 5.7. Allometric scaling exponents, *i.e.* the slope of the relationship between mass-specific DEE and body mass, of different species of chicks. Despite higher initial levels of DEE in more precocial chicks, DEE does not increase more rapidly in the course of development than in more altricial species. Black symbols: this study; grey symbols: precocial black-tailed godwit and northern lapwing, semi-precocial arctic and Antarctic tern (avg) and kittiwkake and altricial savannah sparrow and yellow-eyed junco, all six obtained from the literature. For specifications and references see text.

DEE of these altricial chicks was similar to neonatal RMR of shorebirds chicks of similar body mass (well below shorebird neonatal DEE; Visser & Ricklefs 1993b), and only at the end of the nestling period of the altricial species did their DEE reach a level close to, or just above, the neonatal DEE of shorebird chicks of comparable mass.

DEE levels obtained in this study started out well above RMR levels of neonate shorebirds as measured for a range of species by Visser & Ricklefs (1993) (fig. 5.2). They corresponded closely to DEE levels found in chicks of other species of shorebirds (fig. 5.6), such as black-tailed godwit (*Limosa limosa*; DEE = 1.549 $\times\text{mass}^{1.092}$ (kJ/day, g); Schekkerman & Visser 2001), northern lapwing (*Vanellus vanellus*; DEE = 2.037×mass1.047 (kJ/day, g) Schekkerman & Visser 2001) and red knot (*Calidris canutus*; DEE = 3.105×mass1.078 (kJ/day, g); Schekkerman *et al.* 2003). Chicks of avocets (*Recurvirostra avocetta*) in Germany and Spain, which have similar neonatal body mass to whimbrel chicks and reach a comparable fledgling mass, exhibited mass-specific energy expenditure similar to that of whimbrel chicks (DEE = 2.539×mass – 29.94 (kJ/day, g); Joest 2003).

DEE increased rapidly with development, as indicated by the high allometric scaling exponent (b = 1.38) (fig. 5.7). Precocial chicks invest a large proportion of their resources in development of their muscles to increase locomotory and thermoregulatory function (Starck & Ricklefs 1998, Krijgsveld *et al.* 2001 [chapter 4]). Thus, it is not surprising that their metabolic function develops at a high rate, even more rapidly than that of black-tailed godwit and northern lapwing chicks (b = 1.09 and 1.05 respectively, Schekkerman & Visser 2001). The scaling exponent is, however, unrelated to developmental mode. Scaling exponents for shorebird chicks do not differ consistently from those for other species, including altricial nestlings, which invest more resources in growth and less in mature function (semi-precocial arctic tern (*Sterna paradisaea*) and Antarctic tern (*S. vittata*): $b = 1.31$ on average, Klaassen 1994; semi-precocial kittiwake (*Rissa tridactyla*): $b = 0.85$, Gabrielsen *et al.* 1992; altricial savannah sparrow: $b = 1.27$, Williams & Prints 1986; altricial yellow-eyed junco: $b = 1.66$, Weathers & Sullivan 1991). Thus, although DEE levels are initially high in precocial chicks, reflecting the high costs for locomotion and thermoregulation, DEE does not subsequently increase more rapidly in the course of development than in more altricial species (fig. 5.7).

High DEE in small chicks

Smaller species had higher DEE levels than larger species, for a given body mass. This is in line with the generally higher metabolic intensity of smaller species (e.g., King & Farner 1961) and the fact that, for a given mass, chicks of smaller species are closer to adult size than those of larger species. Relative to the metabolic rates of both neonate and adult shorebirds, chicks of both smaller and larger species showed a high DEE from hatching onward. Relative to their RMR, however, the DEE of chicks of the smaller species exhibited greater mass-specific metabolic increments than that of chicks of larger species. In addition, growth rates of smaller species were higher than those of larger species. Thus, chicks of small shorebird species not only performed at a relatively high energetic level but simultaneously grew at a high rate as well, whereas chicks of larger species performed at a relatively lower level and grew less quickly.

This finding of a positive correlation between function and growth rate contradicts a trade-off between growth rate and mature function postulated by several authors (e.g., Dawson & Evans 1957; Ricklefs 1979; Olson 1992; Konarzewski *et al.* 2000), and suggests that shorebird chicks can modify the relationship between growth rate and mature function considerably. This supports the results of Krijgsveld *et al.* (2001; chapter 4), who demonstrated that catabolic capacity (activity of enzymes citrate synthase, pyruvate kinase and hydroxyacyl-CoA-dehydrogenase) in the skeletal muscles of shorebird chicks, especially early in development, was higher in the smaller and faster-growing chicks of the dunlin than in the larger and slower-growing chicks of the whimbrel. A possible explanation for this lies in the allometric scaling of power requirements for locomotion and the relative thermal inertia of larger chicks, which may result in a reduction of energy demands with increasing size. This is consistent with the idea that precocial chicks of larger species on the arctic tundra are not so much restricted by low arctic temperatures, but are mainly limited in their northern distribution by the time they need to complete growth during the short summer season. In contrast, chicks of smaller species are constrained by low arctic temperatures, which challenge their energetic capacities and require them to work at high metabolic levels.

Little stints (*Calidris minuta*) are similar in size to least sandpipers (neonatal mass both 4 g; adult mass 19-24 g vs 21 in least sandpiper) and belong to the same subfamily of Calidridinae. DEE and growth rate of chicks of little stints was measured in Taimyr (arctic Siberia) by Tjørve *et al.* (2007b). Growth rate of the two species was highly similar (logistic growth constant K was 0.23 and 0.24 for little stint and least sandpiper resp., inflection point 7.4 and 7.7 d). If functional capacity of the chicks were directly related to size and/or growth rate, one would expect a similar level of DEE in the two species. However, although mass-specific DEE of little stints was similar to that of least sandpipers at hatching (both ca. 10 kJ d^{-1}), it increased more rapidly with size and thus reached considerably higher levels than least sandpipers (130–140 kJ d^{-1} at fledging body mass vs. 72 in least sandpiper). This could be related to the lower ambient temperatures at Taimyr than at Churchill (8°C vs. 20°C on average, respectively), resulting in little stint chicks in Siberia operating at higher energy levels. But also dunlin chicks, which are slightly larger than least sandpiper chicks, and thus were expected to have a lower mass-specific DEE, reached higher levels of mass-specific DEE than least sandpiper chicks under the same environmental conditions in Churchill. These results suggest that in comparison to dunlin and little stint, least sandpiper chicks are less able physiologically to meet the energetic demands exerted by ambient conditions in the high arctic. This could explain why their distribution is more limited in the northern regions.

Wind but not ambient temperature affects DEE

Although DEE tended to decrease slightly with increasing ambient temperatures, we found no significant effect of temperature or solar radiation on DEE. For example, the DEE of three dunlin chicks of intermediate mass and measured under the coldest local circumstances (3°C), was similar to the DEE of the other dunlin chicks. Growth rate of these three chicks was however reduced slightly (not significantly) compared to that of the other chicks, which suggests that these chicks may have been foraging less than would be required to sustain growth, and which may have been possible as a result of artificial food provision and indoor housing. No relation between growth and ambient temperatures was observed for the other species. Tjørve *et al.* (2008) also found no effect of ambient or operative temperature on DEE of chicks of Kittlitz's plovers, blacksmith lapwings or crowned lapwings in Africa, while Schekkerman & Visser (2001) showed a decrease in DEE with increasing temperature for godwit chicks but not for lapwing chicks under similar weather conditions. Under lower arctic temperatures, Schekkerman *et al.* (2003) showed that DEE of knot chicks increased with decreasing ambient temperatures, but not with wind speed.

An explanation for the observed lack of effect of ambient temperature on DEE may be that the amount of heat produced by locomotion is enough to sustain thermoregulation under most circumstances. Because ambient temperatures were relatively high during our study, this may well have been the case. Furthermore, when ambient temperatures are low, chicks spend more time brooding and less time foraging (Beintema & Visser 1989b, Krijgsveld *et al.* 2003b [chapter 6]). More brooding reduces energy expenditure at low temperatures (Krijgsveld *et al.* 2003a; chapter 7), which may counterbalance the effect of cold to increase thermogenesis. This may also explain why DEE was lower when night-time hours comprised a larger proportion of the measurement period, more so than the observed effect of wind speed, but no data on nocturnal brooding behaviour were available to test this. When ambient temperatures are lower, chicks would need to spend more energy in order to sustain growth, and under those circumstances DEE might increase at lower ambient temperatures.

When wind speeds were higher, DEE levels did increase slightly. Bakken *et al.* (2002) showed that natural variation in wind speed had a substantially larger effect than T_a on thermal conductance of shorebird chicks in Churchill. Thus, whereas T_a's, which were relatively high for an arctic environment, may not have been low enough to exert an effect on DEE, higher wind speeds did increase DEE through reduced skin temperature and relatively high evaporative water loss (Bakken *et al.* 2002).

Heat production through locomotion as well as shivering

DEE was similar to cold-induced PMR. This is surprising, as DEE is generally expected to lie below PMR. Part of the explanation may be that PMR was measured by inducing maximum thermogenic capacities, which was achieved by exposing the chicks to low temperatures (Ricklefs & Williams 2003). Several studies have shown that heat generated during locomotion substitutes thermoregulatory costs (e.g., Zerba & Walsberg 1992, Bruinzeel & Piersma 1998, Marjoniemi *et al.* 2001). As the chicks were not mobile in the metabolic chamber, heat had to be produced almost entirely by shivering. Especially in younger chicks, which have limited functional capacity, this is likely to have limited heat generation and therewith the level of PMR in comparison to free-living chicks, where energy expenditure may be higher as a result of locomotory activity. Thus, measured PMR would be reduced below the PMR that chicks would have been able to achieve under free-living conditions where energy for locomotion adds to thermoregulation. However, small shorebird chicks often are near their limits of temperature regulation, and thus can be expected to generate heat at a near maximal rate, without a substantial metabolic reserve.

Most animals retain, or can rapidly generate, reserve metabolic capacity (Diamond & Hammond 1992; Toloza *et al.* 1991; Piersma & Lindström 1997; but see Suarez *et al.* 1997). PMR in small shorebird chicks may be limited by developmental constraints on muscle tissue. As the chicks grew, the reserve metabolic potential increased, as indicated by the increasing difference between mass-specific PMR over DEE. This was especially true for chicks of least sandpiper and dunlin, where the increase in reserve metabolic potential with body mass was largest. This is likely to be related to the rapid growth of the pectoral muscles of these species later in the chick stage (Krijgsveld *et al.* 2001 [chapter 4]; Marjoniemi & Hohtola 1999). The reserve metabolic potential is not used during normal foraging, especially in fair weather conditions such as in Churchill during this study, but it is stimulated in the cold metabolism chamber.

Overall, the chicks of small arctic sandpipers, which are among the smallest homeotherms, are remarkable for maintaining high levels of metabolic activity while also growing rapidly. The chicks of larger species also grow rapidly to achieve large size during the brief arctic growing season, but their lower thermal conductance and heat loss results in a lower daily energy expenditure per gram body mass. Although locomotion contributes to heat production, the higher daily energy expenditure per gram of the chicks of smaller species is more closely related to thermogenic considerations than to foraging. Thus, smaller species are likely more sensitive to variation in temperature and wind speed than larger species, and these environmental conditions undoubtedly limit the northern distributions of these species.

Acknowledgements

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Part 3

Behavioural adaptations: foraging behaviour and body temperature

Chapter 6

Time budgets and body temperatures of American golden plover chicks in relation to ambient temperature

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Abstract

We studied time budgets of precocial chicks of American golden plovers (*Pluvialis dominica*) on the tundra near Churchill, Manitoba, Canada, to assess how time budgets are influenced by environmental and body temperatures. Foraging time per day increased with increasing ambient temperatures and levels of solar radiation, as well as with age. This increase was due to an increase in the length of foraging bouts (*i.e.* the period of time in between two brooding bouts). The length of brooding bouts averaged 12 min, independent of ambient conditions or age. Body temperatures were lower under colder environmental conditions and increased as the chicks grew older. Based on measurements of cooling rates of penned chicks, we determined that at the end of a foraging bout, body temperature never fell below 35.5°C, which is high for a precocial chick. We suggest that in Churchill, American golden plover chicks are not limited in their foraging time by ambient conditions, and they can collect sufficient food in the short periods of foraging that are available to them to sustain normal growth. By minimizing foraging bout length in favor of parental brooding, chicks may increase their digestive efficiency as well as save energy that would otherwise be expended on thermoregulation and locomotion.

Introduction

The foraging behavior of precocial shorebird chicks is strongly affected by weather conditions. Young chicks forage by themselves, but as they are not yet homeothermic they lose body heat while foraging and must be brooded by their parents at regular intervals to be rewarmed. On the arctic tundra, where many shorebird species breed, the weather is often adverse, and this results in reduced time for the chicks to forage (Theberge & West 1973, Boggs *et al.* 1977, Beintema & Visser 1989b). The way in which food availability and ambient temperatures together affect foraging time, ultimately determines the northern limits of the breeding distribution. To understand this limitation, we need to understand how these factors determine foraging time.

Precocial chicks can remain mobile at reduced body temperatures (Norton 1973), which enables them to continue foraging while they are cooling. However, body temperatures below a certain threshold impair locomotion (Norton 1973, Myhre & Steen 1979, Pedersen & Steen 1979) and require that the chicks must be brooded. Accordingly, body temperature should affect foraging time, as suggested by Pedersen & Steen (1979) and Chappell (1980). Because a chick cools faster when the ambient temperature is lower (Visser & Ricklefs 1993b), the body temperature threshold would be reached earlier under colder conditions, which would thus restrict the available foraging time. Other factors may also play a role in determining the available foraging time, apart from or interacting with the chick=s body temperature. For example, digestive rate could limit the length of a foraging bout at the time a chick=s stomach is filled. To date, we know little about the way in which physiology and behavior determine the foraging time available to a precocial chick. This study investigates the importance of body temperature in determining foraging time under fluctuating ambient conditions.

We studied the time budgets and body temperatures of both penned and free-living chicks of American golden plovers (*Pluvialis dominica*) on the subarctic tundra near Churchill, Manitoba, Canada. Under varying weather conditions, we determined the total time available for foraging and assessed the length of foraging and brooding bouts as well as the body temperature at which chicks ended a foraging bout. These results were then compared to evaluate the importance of low body temperature, and its interaction with other factors such as age and environmental conditions, in determining the foraging time of shorebird chicks.

Methods

Study area and subjects

The observations and measurements were performed in 1997 and 1998 on the subarctic tundra near Churchill, Manitoba, Canada (58°45'N, 94°04'W). This location is at the southernmost border of the breeding range of the American golden plover (Glutz von Blotzheim *et al.* 1971). In Churchill, American golden plovers are common breeders (see also Jehl & Smith 1970) on hummocks and ridges with short, lichen-dominated vegetation (Byrkjedal & Thompson 1998). We observed a total of eight families with four chicks each and one family with three chicks. Average hatching date was 7 July, which is normal for the area (JR Jehl Jr, pers. comm.). Observations and collection of eggs were carried out under permit from the Canadian Wildlife Service (permit nos. WS-M44B and CWS98-M038a). Husbandry and laboratory procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri–St. Louis, St. Louis, Missouri.

Environmental conditions

To correlate thermal properties of the environment with chick behavior, environmental temperatures were recorded continuously throughout the season. Two 3.5-cm spheres, one white and one black, with internally mounted thermocouples, were positioned 10 cm above ground in a micro habitat characteristic of foraging American golden plover chicks. The white sphere measured ambient air temperature (T_a). The black sphere provided an approximation of the thermal environment with wind and solar radiation factored in, although not necessarily in the same fashion as experienced by the chick (Bakken *et al.* 1985, Walsberg & Weathers 1986). By subtracting the white sphere temperature from the black sphere temperature, we obtained a measure of radiative-convective load, independent of T_a. Levels thus obtained closely matched levels measured for comparison with a pyranometer (ANOVA: $F_{1,\,117} = 623.7$, $P < 0.001$, $r^2 = 0.84$; LI-200SA, Lincoln, NE, USA). Wind speed was measured 10 cm above the ground with a cup anemometer (A100L2, Grant Instruments Ltd., Barrington, England), which was capable of measuring wind speeds ranging from 0 to 75 $\mathrm{m} \times \mathrm{sec}^{-1}$. The climate data were averaged over intervals of 15 min and recorded with a Squirrel 1204 data logger (Grant Instruments Ltd.).

Behavioral observations

Observations on the foraging behavior of free-living plover families were made from a blind or a vehicle at a distance of 100–200 m. Families occasionally moved toward the observer to distances as little as 5 m. To enable visual recognition, all chicks were marked individually within the family with red or yellow dye on the white down of the breast or circumcloacal region at the time when the chicks were caught (see next paragraph).

Chicks were not always in sight. To be able to infer whether a chick was foraging or being brooded at these times, we used temperature-sensitive transmitters that were mounted externally on the backs of chicks. For this purpose all four chicks of a family were caught shortly after the fourth chick of the clutch hatched. At this time the chicks still return to the nest for brooding, and thus can be caught simultaneously. We caught the chicks by waiting from a distance until all four chicks were being brooded by the adult, and then running to nest. The adult then flies off, but the chicks hunker down at or close to the nest and can be collected. The procedure of measuring the chicks and attaching the transmitters took no more than 15 min, after which they were put back in the nest, and we left the area. The adult consequently

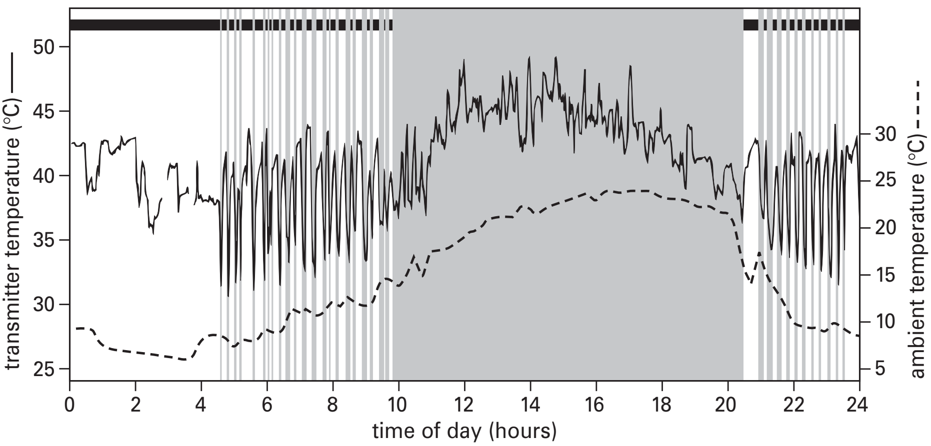

Figure 6.1. Example of transmitter temperature (solid line) of a 3-day-old American golden plover chick throughout the day, indicating foraging and brooding behavior. Foraging bouts are shown as shaded vertical bars. Brooding (dark grey horizontal bar) complements foraging. Ambient temperature is plotted as a dotted line. Between 10:00 and 20:30, high ambient temperatures rendered transmitter temperatures unreliable, but direct observation showed that chicks were foraging continuously during this period.

returned to the nest within minutes. In each observed family, two chicks were equipped with a transmitter. When hatching order could be determined, we attached transmitters to the second and third chicks of the brood.

The behavior of the chicks was classified by combining visual observations with transmitter temperatures. This way, we could reliably monitor most brooding and foraging behavior of at least two chicks of a family, regardless of weather conditions or visibility. The two methods thus complemented each other and resulted in a good coverage of foraging behavior. When a chick carrying a transmitter started foraging, transmitter temperature dropped markedly, whereas at the start of a brooding bout it rose again. This process is depicted in figure 1, for data between 5:00 and 9:00 and between 21:00 and 24:00. Brooding and foraging bouts could be determined precisely from these rapid changes in transmitter temperature, even when the chick was out of sight. During warm spells or when solar radiation was high, the transmitter heated up to such an extent during foraging bouts that it was impossible to conclude from transmitter temperature whether a chick was foraging or being brooded. Transmitter data were excluded when the ambient temperature was too high to determine the behavior of the chick with certainty, but since chicks were often more active at these higher temperatures, they could be followed well visually, and behavior could still be classified. This is shown in figure 6.1 for the data recorded between 10:00 and 20:00. Since the chick could be seen foraging during this period, behavior could be classified as foraging.

Observations in 1997 were made 24 hr per day, which revealed that chicks did not forage between 23:00 and 03:00, while it was dark (fig. 6.1, see Results). In 1998 observations were therefore restricted to daylight hours from 03:00 until 23:00. The nine broods were followed over a total of 45 days, making a total of 500 hr of observation time. Since a family could not always be found, or temporarily disappeared from sight or transmitter range, sample sizes differ per age and temperature class, and are given in the figure legends. The amount of observation time used to calculate foraging percentages was at least 1 hr but averaged 16.4 hr per age and temperature class. Behavior and transmitter temperature were recorded every 2 min for each chick and both parents when they were in sight. Chick behavior was categorized as either brooding or foraging; the latter including all non brooding behavior. Time budget analysis was based on all daytime observations. Analysis of the length of foraging and brooding bouts was based only on those bouts for which both start and end were known.

Temperature transmitters

Temperature-sensitive transmitters were used only to differentiate between foraging and brooding behavior. Transmitters (type BD-2AT supplied by Holohil Systems Ltd., Carp, Ontario, Canada) weighed 0.68 g (3.7% of neonatal body mass) and were 13×6×3 mm in size with a flexible antenna of 16 cm. They were attached with cyanoacrylate glue to the upper back of the chick just behind the neck. Transmitters remained in place for ca. two weeks. Chicks were not hindered by the transmitters. The added mass of the transmitter lies within the normal weight variation among chicks and for individual chicks throughout the day (Byrkjedal & Thompson 1998, chapter 2 of this thesis), thus the metabolic costs of carrying a radio are small. Chicks with transmitters grew normally, moved along naturally with the family, never got caught in the vegetation, covered similar distances while foraging as chicks without transmitters, and showed no difference in bout lengths (GLM, residual analysis: no significant effect of carrying a transmitter on bout length (foraging: $F_{1,\,968} = 2.6$, $P > 0.05$, $r^2 = 0.003$; brooding: $F_{1,\,897} = 2.3$, $P > 0.05$, $r^2 = 0.004$).

The temperature measured by the transmitter was intermediate between the temperature of the chick=s skin and the air temperature, and thus did not measure body temperature. Each transmitter sent out a signal at a characteristic rate that could be picked up with a radio receiver carried by the observer. The signal rate was temperature dependent and was calibrated in a water bath against a mercury thermometer prior to attachment and when possible after recollection. Signal rate was determined manually by recording the time to receive 10 pulses. The signal could be received up to 500 m, but became faint when the chick moved behind a slope or a rock.

Body temperature

To measure body temperature (T_b) of chicks during foraging bouts, we handreared seven chicks in 1998 from eggs collected in the field and hatched in an incubator. One day after hatching, the chicks were moved to an outside enclosure. The enclosure was circular with a diameter of 10 m, and surrounded by a chicken-wire fence 50 cm high, lined along the lower 20 cm with cloth and plastic, and fixed firmly to the ground with tent pegs to prevent escapes. A cover of large mesh netting kept out predators. An artificial brooder provided heat to the chicks. It consisted of a wooden box of 20 (height) × 30 (depth) × 20 (width) cm, with an entrance of 15×15 cm, in which a light bulb and a thermal blanket were placed, maintaining a temperature of up to 41°C closest to the light bulb. The light from the bulb served to direct the chicks to the brooder. Chicks learned to enter the brooder to be rewarmed within two days. From that day forward they were left in the enclosure continuously. Because naturally available food diminished rapidly in the enclosure, food and water were supplied daily. Food consisted of turkey pre-starter mix (Puratone Corporation, Niverville, Manitoba, Canada), supplemented with a mix of tuna, chicken, oatmeal, and boiled eggs, as well as with freshly caught mosquitoes. Composition of the nutrients resembled natural insect food. Food was scattered on the ground to stimulate chicks to spend time foraging.

Foraging behavior was observed and T_b was measured from within the enclosure, where the observer sat quietly on the ground. A minimum of 4 and a maximum of 8 individually color-banded chicks were followed simultaneously in the enclosure. Chicks were not disturbed by the presence of an observer, and often approached to catch mosquitoes that were attracted by the observer. Time budgets were determined by recording when the chicks entered and left the brooder. T_b was measured by quickly picking up the chick and inserting a greased, very thin thermocouple wire (30 gauge, tip dipped in a drop of nail polish to cover the sharp end), attached to a digital thermometer (Omega, Laval, Canada; accuracy 0.1°C) 1 cm into the cloaca. T_b was not measured more than once every half-hour in each chick, both during foraging and during brooding. After a T_b-measurement, behavior of the chick was not recorded for 5 minutes to allow the chick get back to its normal routine. Behavior of the chicks was not affected by the measurement. Chicks were released in a healthy condition in their natural environment at the end of the study, around their fledging age (22 days).

Calculation of cooling rates

The availability of the artificially supplied food may have altered the behavior of the chicks, enabling them to stop feeding at a higher T_b than free-living chicks. Because of this, T_b measured in the enclosure could not be used to measure T_b at the end of a foraging bout. Instead, measurements of cooling rates and foraging bout lengths were combined to estimate this value. The cooling rates of chicks were calculated by subtracting the amount of heat lost through wet thermal conductance from the metabolic heat production of the chick (following eq. 5 in Visser & Ricklefs 1993b). Metabolic measurements were taken from unpublished data of JB Williams & RER. Briefly, standard (SMR) and peak metabolic rates (PMR) of American golden plover chicks of 1 to 20 days old were measured in a parallel laboratory study using an open-circuit respirometer. Temperature was initially maintained within the thermoneutral zone to obtain an estimate of SMR and then was decreased by about 0.5°C per min until metabolism reached PMR and subsequently began to decrease. T_b and evaporation were monitored continuously throughout the trials. These measurements provided us with data for PMR and for the change in metabolic rate with the subsequent reduction in T_b, as well as with data for the wet thermal conductance, assuming a specific heat of $3.45\ \text{J} \times \text{g}^{-1} \times {}^{\circ}\text{C}^{-1}$ (Hart, 1951). Using these detailed data on PMR and the changes in SMR with T_b, and knowing the foraging bout lengths, we could then, for each specific age and T_a, estimate the decrease in T_b of a chick during a period of time similar to the measured foraging bout length. Thus we obtained an estimate of the T_b at the end of a foraging bout for each age and T_a.

Statistical analyses

Data were analyzed using SPSS version 7.5 (SPSS Inc. 1997). Tests were performed as much as possible within a single model, using general linear models (GLM). Age, T_a, radiative-convective load, and wind were entered as covariates; time of day and nest as fixed factors. For each separate analysis, the statistics of the overall model are given, generally combined with the statistics for the individual covariates and factors. Foraging percentages were arcsine transformed prior to analysis, and percentages were calculated from the observations by grouping the data into classes of 5°C per age. Data on bout lengths were log transformed. Values reported are means, except for average bout lengths, where we calculated geometric rather than arithmetic means because the distributions of foraging and brooding bout lengths were strongly positively skewed.

Results

Environmental temperatures

Ambient temperatures in Churchill in July fluctuated widely (fig. 6.2). The monthly average was 18.7°C in 1997 and 15.0°C in 1998, which was considerably higher than the long-term average of 12.0°C (period from 1943–2000; source: Winnipeg Climate Centre, Winnipeg,

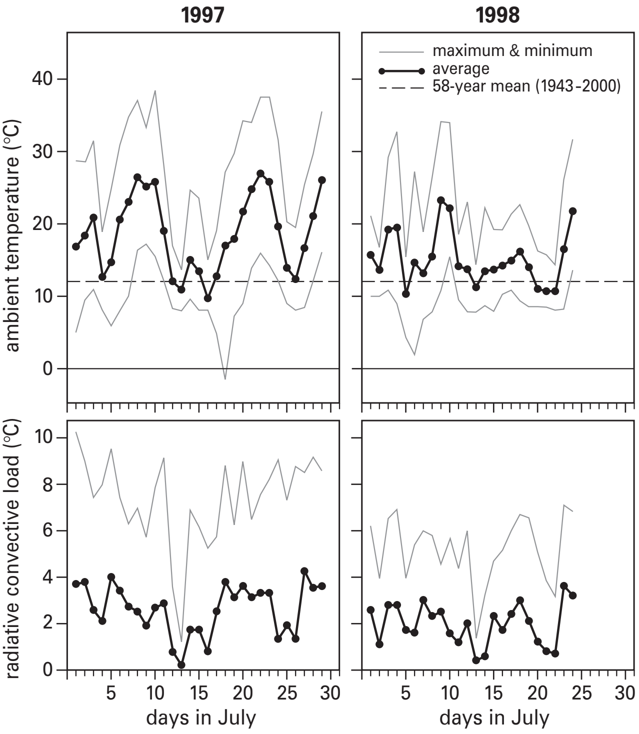

Figure 6.2. Ambient temperatures (upper panels) and levels of radiative convective load (indicating solar radiation; lower panels) in Churchill, Manitoba, Canada, in July 1997 and 1998. Daily averages (filled circles) are shown, as well as daily maxima and minima (grey lines). Mean ambient temperature from 1943 to 2000 was 12°C (dashed line).

Manitoba, Canada). For comparison, the summer of 1992 was much colder: the mean ambient temperature in July 1992 was 7.5°C, with an average maximum of 12.6°C and an average minimum of 2.3°C. The monthly minimum and maximum during our study were –1.4°C and 38.4°C respectively, both recorded in 1997. Like T_a, the radiative-convective load was higher in 1997.

Time budget

Foraging activity started from 03:00 in the morning, just after first daylight (sunrise at ca. 03:30), and continued until dark at around 22:00 to 23:00, when the chicks spent an increasing amount of time brooding. From 23:00 onward all foraging activity ceased and transmitter temperature was continuously at brooding level, only occasionally dropping for a minute, likely due to a shift in position of either parent or chicks, or because parents switched brooding duties. Consequently, a maximum of 20 hr per day were available for foraging (03:00–23:00). Transmitter and ambient temperatures as well as the lengths of foraging and brooding bouts are plotted in figure 6.1 as an example. Of the available 20 hr per day, the percentage of time that the chicks foraged increased with increasing T_a and with increasing age of the chicks (fig. 6.3; GLM: overall model: $F_{2,\,43} = 48.8$, $P < 0.001$, $r^2 = 0.69$; foraging % was significantly correlated with T_a [$F_{1,\,43} = 10.3$, $P < 0.01$] and with the interaction between T_a and age [$F_{1,\,43} = 54.4$, $P < 0.001$]). The increase in foraging time with age was fitted with logistic regression for separate temperature classes (of 5°C or 10°C, see fig. 6.3), giving significant fits ($P < 0.001$) for all classes except the coldest (0–5°C; fig. 6.3). Pearson = s r was 0.30, 0.29, 0.34, 0.38, 0.44 respectively for increasing temperature classes from 5–10°C to 30–40°C.

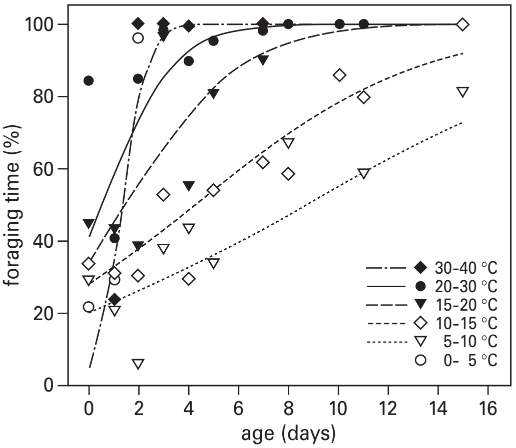

Figure 6.3. Time spent by free-living American golden plover chicks on foraging and other activities resulting in body cooling, in relation to the age of the chicks and ambient temperature. Ambient temperature was grouped into six classes. Foraging time was calculated as a percentage of the active day (*i.e.* between 03:00 and 23:00). Averages are based on 500 hr of observation time on 9 families of golden plovers, averaging 80 hr per day of age). Lines depict regressions for the upper five temperature classes, obtained by logistic regression.

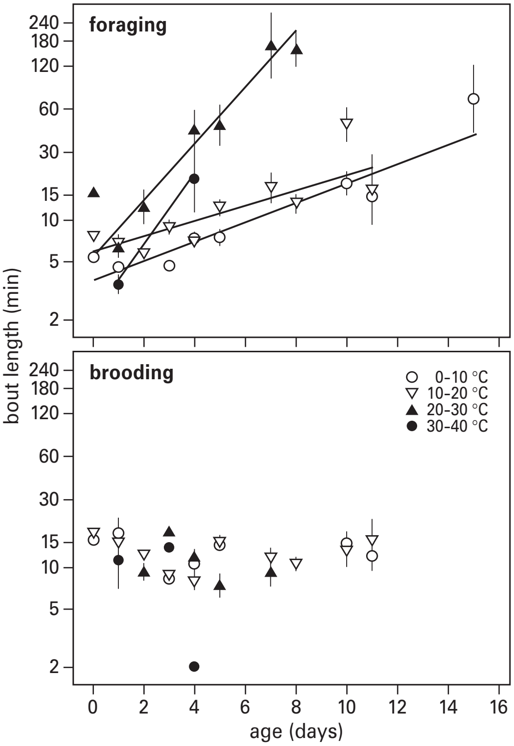

Figure 6.4. Mean length ± se of foraging and brooding bouts in relation to age of American golden plover chicks and ambient temperature, grouped into four classes. Symbols indicate geometric means. Lines depict significant linear regressions on log-transformed data. Sample size is 1002 foraging bouts and 899 brooding bouts (35 bouts per age per temperature class on average) recorded from 9 families of golden-plovers.

Bout lengths

Brooding bouts lasted 12 min on average during daytime (sd of geometric mean = –6/+13; range 2–302 min; n = 899), and did not vary with respect to age or environmental conditions. Foraging bouts (the period of time between two brooding bouts) lasted ca. 7 min in chicks up to 2 days old, but bout length increased rapidly as the chicks grew older and as T_a increased (fig. 6.4). In addition to T_a, windspeed and radiative-convective load also significantly influenced the length of the foraging bouts, as did time of day (table 6.1; $r^2 = 0.48$).

Foraging bouts were considerably longer between 06:00 and 11:00 hr than during other parts of the day, and were shortest just after sunrise and before sunset (fig. 6.5). The ratio between the foraging bout length observed and the foraging bout length predicted on the basis of age and T_a, had a very stable value of 1 to 2, except between 07:00 and 10:00, when it peaked to a maximum of 8. This indicates that bout length peaked during midmorning regardless of age and T_a. At night, chicks were brooded continuously up to 10 days of age, and consequently always showed a high transmitter temperature (fig. 6.1). Chicks older than 10 days were not always fully covered by the parent because of their large size. Because of this, temperature of the transmitter would drop due to insufficient covering by the parent, giving the impression that the chick was foraging. In addition, by 15 days chicks were no longer brooded

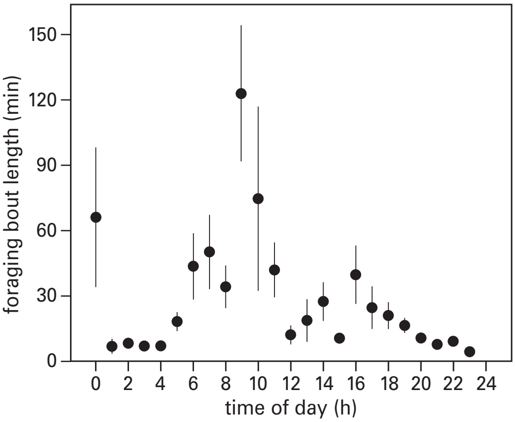

Figure 6.5. Mean length ± se of American golden plover chick foraging bouts in relation to the time of day. Data include nighttime observations. The longer foraging bouts at 00:00 reflect resting behaviour of older chicks that are not being brooded anymore, and does not reflect foraging, which does not occur at night in younger chicks. Sample size is 1054 bouts (44 bouts per age on average), recorded from 9 families of golden-plovers.

Table 6.1. Factors that affect the foraging bout length of American golden plover chicks, shown by the results of a general linear model on the logarithm of foraging bout length. *** indicates $P < 0.001$.

Source	Type III Sum of Squares	df	*F*
model	109.4	33	26.9***
intercept	13.4	1	108.8***
age	17.5	1	142.1***
radiative-convective load	5.3	1	42.9***
wind speed	7.7	1	62.3***
age × radiative-convective load	13.4	1	108.7***
T_a × radiative-convective load	12.7	1	12.7***
T_a × wind speed	14.6	1	118.5***
time of day	6.8	19	2.9***
nest	6.3	8	6.4***
error	119.3	968	

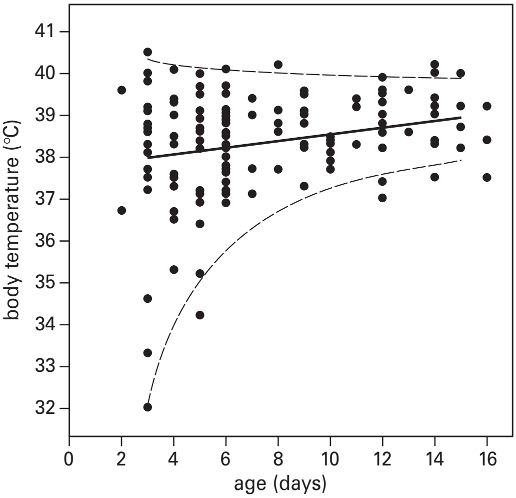

Figure 6.6. Body temperatures of American golden plover chicks during foraging in an outdoor enclosure. Lines depict the regressions of minimum, maximum (grey lines, fitted with inverse function) and mean (solid line; linear function) temperatures.

at night, but were seen lying close by the parent, which also resulted in lower transmitter temperatures. This is shown in figure 6.5 as a longer foraging bout length at night, but reflects brooding and resting behavior. The number of foraging and brooding bouts per hour ranged between 0.25 and 3 bouts per hour. The number of bouts increased with lower ambient temperatures, and decreased with age (GLM: number of foraging bouts versus age and T_a; overall model: $F_{2,10} = 15.2$, $P < 0.01$, $r^2 = 0.75$).

Body temperature

The T_b of chicks foraging in an outdoor enclosure varied widely (fig. 6.6). The minimum T_b measured in the chicks was 32°C at 3 days of age. This minimum increased as the chicks grew older, and did not drop below 37°C after 6 days of age. Average T_b increased slightly with age (linear regression, $F_{1,144} = 10.2$, $P < 0.01$, $r^2 = 0.07$), and the range over which body temperature varied decreased until the chicks were 6 days old, after which it remained more or less stable. Body temperature was significantly higher when T_a was higher, even in chicks over 8 days old that already have a high degree of homeothermy. A higher radiative-convective load increased the slope of this relationship, as did younger age (GLM: overall model: $F_{4,\,141} = 34.0$, $P < 0.001$, $r^2 = 0.49$; significant effects of T_a [$F_{1,\,141} = 11.9$, $P < 0.01$], of the interaction between T_a and age [$F_{1,\,141} = 67.3$, $P < 0.001$], of the interaction between T_a and radiative-convective load [$F_{1,\,141} = 64.7$, $P < 0.001$], and of the interaction between T_a, age and radiative-convective load [$F_{1,\,141} = 48.3$, $P < 0.001$]).

Body temperature at the end of a foraging bout was estimated by combining the calculated cooling rate of the chicks with the mean foraging bout length observed. Based on the calculations we found that T_b never dropped below 35°C, regardless of age or T_a (fig. 6.7). In general, minimum T_b increased with warmer T_a and as the chicks grew older. However, chicks over 1 day old tended to let their T_b drop further when T_a was 5–10°C than when T_a was 1°C. The bout length used for calculating T_b was based on the regression between foraging bout length and age and T_a. Because this regression gives only an estimate of true bout length, the calculated T_b at the end of a foraging bout also gives only an estimate of the true T_b. For comparison, the T_b values measured at the end of a foraging bout in chicks foraging in the enclosure are also plotted in figure 6.7, showing that actual minimum T_b in the enclosure was equal to or higher than the calculated value of minimum T_b in chicks of 3 and 8 days old. Only in chicks of 15 days old did we find some minimum T_b values that were lower than the calculated T_b.

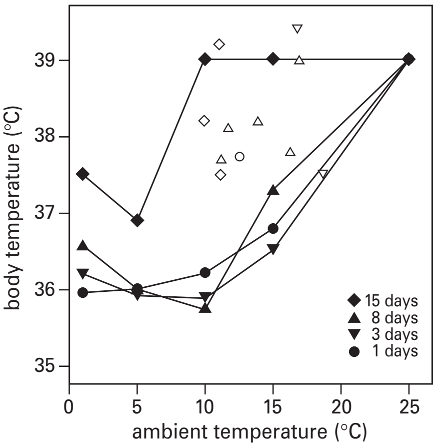

Figure 6.7. Body temperatures of American golden plover chicks at the end of their foraging bouts, calculated from their cooling rates in relation to ambient temperatures. Each symbol represents the body temperature at the end of a foraging bout, for a specific ambient temperature (x-axis) and for a specific age (shaded symbols). Lines connect similar ages. As a comparison, unshaded symbols show the measured body temperatures of chicks at the end of a foraging bout in the enclosure; ages for these values are indicated by shapes as in the legend.

Discussion

Foraging time

Ambient temperatures in Churchill fluctuated considerably within a breeding season. Chicks experienced relatively warm summers in both 1997 and 1998. Our observations indicate that in 1997 and 1998, with an average T_a of 17°C, a 3-day-old American golden plover chick in Churchill had 60–65% of the day available for feeding (excluding nighttime; calculation based on regression). At the more typical (58-year average) T_a for July (12°C), foraging time would decrease to ca. 40%. Given that American golden plover chicks hatch at the beginning of July, and that they are particularly vulnerable to low T_a until they are ca. 10 days old, T_a during 1-20 July is most critical. During this period, the average T_a was below 10°C for eight days (40%) each year, on average, over the 58 years for which temperature recordings are available. This implies that during 40% of the time, a 3-day-old chick=s foraging would be limited to less than 30% of the day.

The large fluctuation in T_a in Churchill is reflected in a similarly large fluctuation in available foraging time. On cold or windy days, growth of the chicks would be reduced or halted (Beintema & Visser 1989b), which could result in death if the weather were unfavorable for several days in a row. Although ambient temperatures at Churchill generally provide enough foraging time for a plover chick, long spells of cold weather are not uncommon (e.g., 1992). Churchill is at the southernmost edge of the distribution of breeding American golden plovers, and postnatal development is thus relatively unconstrained by climate. At higher and colder latitudes, less time is available for foraging. For example, on Southampton Island (64°N, 83°W) the average T_a in July is 9°C (data from Environment Canada, Ottawa, Ontario, Canada), which corresponds to 30% of the active day available for foraging for a 3-day-old chick. At Barrow (71°N, 156°W), the northernmost breeding range of the plovers, the mean T_a in July is 4°C (data from the Alaska Climate Research Center, Fairbanks, AK), which reduces foraging time even further. Apparently even this small amount of time is enough for the chicks to fledge. Naturally, summer days are longer farther north, which partly balances loss of foraging time. However, whether a chick can fully use this longer day, or whether it forgoes foraging to sleep or because insects are less available during certain parts of the day, is not known.

Although T_a and age of the chick can largely explain foraging bout length, foraging bouts were exceptionally long during mid morning. At this time, T_a generally increased rapidly. After the cold nighttime and early-morning hours, chicks may use this increase in T_a, the associated reduction in thermoregulatory costs, and increased insect abundance (chapter 3) to fill their stomachs after the night-time period without foraging.

Ambient temperature and bout length

In response to low T_a, American golden plover chicks reduced the length of their foraging bouts and increased the number of bouts. Although T_a did have a strong effect on foraging time, the relatively moderate temperatures at Churchill do not appear to limit the foraging time of American golden plover chicks. Our observations suggest this in a number of ways. First, instead of foraging for approximately the same length of time at a specific T_a, the lengths of foraging bouts varied widely, as shown by the low r^2 of the regression of foraging bout length with age and T_a. This indicates that environmental conditions are not the only determinant of the time activity budget of the chicks. Second, the increase in foraging bout length between 06:00 and 11:00 suggests that chicks were able to lengthen their foraging bouts when conditions other than T_a were favorable. If T_a were a limiting factor to the foraging time of the chicks, T_a would control bout length, and such an increase in bout length with time of day would not occur. Third, growth rate of the chicks in the field was as high or higher than that of chicks raised in the lab. Body masses of 16 chicks reaching ages over 3 days in the field were, with one exception, at or above the average mass of handraised chicks (chapter 2). Thus, foraging time apparently was sufficient for the chicks to satisfy their food requirements.

Body temperature and bout length

Body temperature of the chicks in the enclosure fluctuated considerably. It increased as the chicks grew older, which is consistent with observations on other species (Bunni 1959, Pedersen & Steen 1979, Prinzinger *et al.* 1991), and decreased when the weather was colder. Minimum T_b at which a foraging bout ended also was lower on colder days. This corresponds roughly with the expectation that chicks cool faster when it is cold and consequently curtail foraging bouts, or cool further, or both. Although precocial chicks can lower their T_b considerably, low T_b involves such costs as reduced growth rate (Koskimies 1950, Rheinwald 1971, Beintema & Visser 1989b). As the summer is short in northern regions, growth rate is important to a chick and thus may favor keeping T_b as high as possible. Secondly, when chicks become too cold, they lose their locomotory ability. Thus, T_b sets an upper limit to the end of a foraging bout (Pedersen & Steen 1979, Chappell 1980). However, minimum T_b measured in this study was high compared to the T_b of foraging precocial chicks in other studies. The T_b at the end of a foraging bout rarely dropped below 35.5°C, as shown by the T_b of the chicks in the enclosure as well as by the calculations of cooling rates of chicks. Several studies indicate that the T_b at which locomotion of precocial chicks becomes hampered lies well below 35.5°C (Norton 1973, Aulie 1979, Myhre & Steen 1979, Pedersen & Steen 1979, Gdowska *et al.* 1993). Thus, the T_b at which mobility starts to be hampered lies below the minimum T_b at which we found the chicks to cease foraging. It is therefore unlikely that T_b alone determines foraging bout length, although it may become more important when the weather is colder and cooling rates of the chicks are higher.

Minimum T_b was not fixed at one set point, but fluctuated with T_a and age. If low T_b were a proximate cause for the chicks to stop foraging, one would expect foraging to continue until T_b had reached a certain set point. The fact that it instead fluctuated with T_a, further suggests that T_b alone does not determine foraging bout length. If bout lengths were constrained by an upper limit of, for example, body cooling, then the distribution of the data would be cut off beyond a certain maximum, resulting in a distribution with a strongly negative skew. However, data were strongly positively skewed. This again suggests that the chicks often return to be brooded before they have reached the maximum bout length permitted by body cooling.

Other determinants of bout length

We have shown that although T_b is an important factor in foraging behavior, it is not the main determinant of foraging bout length of American golden plover chicks exposed to moderately low T_a. The rate of digestion may also contribute to ending a foraging bout. Insects are digested relatively slowly (Speakman 1987, Afik & Karasov 1995). If digestion generally lasts longer than a foraging bout, the stomach of the chick would be filled up after a certain time of foraging, forcing the chick to stop foraging. Since digestive efficiency is lower when T_b is lower (Kleiber & Dougherty 1934, Osbaldiston 1966), the rate and efficiency of digestion will increase when a chick is brooded and T_b is increasing. Because young chicks generally have a lower digestive efficiency than adults (Norton 1970, Karasov 1996), any behavior that increases digestive efficiency may play an important role in the foraging of shorebird chicks. In addition, the chick will save energy while digesting during brooding.

Another factor in ending a foraging bout is the balance between energetic costs and benefits of foraging. During a foraging bout, the chick cools down, which may suppress the chick = s mobility and rate of food intake. Simultaneously, the metabolic rate of the chick increases (JB Williams & RER, unpublished data). Thus, as the chick continues to forage, energy expenditure will at some point start to outweigh energy intake, at which time the chick should end its foraging bout. During foraging, the energy expenditure of a chick is high (Schekkerman & Visser 2001) and close to the maximum cold-induced and exercise-induced metabolism (JB Williams & RER, unpublished data). Thus, by minimizing foraging time and increasing brooding time, a chick can considerably reduce its energy expenditure. Experimental work on the relationships between T_b, food intake, digestion, and energy expenditure under varying ambient conditions is needed to determine their roles in foraging behavior.

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Chapter 7

Foraging behaviour and physiological changes in precocial quail chicks in response to low temperatures

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Abstract

We examined whether low ambient temperatures influence foraging behavior of precocial Japanese quail chicks and alter the balance between investment in growth and thermogenic function. To test this, one group of chicks was exposed to 7°C and one group to 24°C during foraging, throughout the developmental stage. Chicks adapted well to the temperatures through a high flexibility in behavior and physiological development. In response to cold, chicks shortened foraging bout lengths two- to sixfold, and increased cycle lengths (*i.e.* length of a brooding bout plus subsequent foraging bout), resulting in a decrease in total foraging time. Body temperature during foraging was lower in cold-exposed chicks, but did not drop below 37.8°C, suggesting that the direct cause to end a foraging bout was not body temperature. Metabolic rate of cold-exposed chicks was reduced by 48 to 60% when switching from foraging to brooding, which may be an important factor in determining foraging behavior of precocial chicks. Mass-specific food intake of the cold-exposed chicks exceeded that of warm chicks by 15%. Cold-exposed chicks doubled foraging efficiency to reach this intake during their reduced foraging time. Metabolic rates initially were similar in both groups, but increased rapidly and were elevated in cold-exposed chicks from 15 days of age onward. Growth rate on the other hand initially was reduced in cold-exposed chicks, and exceeded growth of warm chicks only after 21 days of age. These results suggest that in response to cold, a shift occurs in the balance between growth rate and thermoregulatory function, in favor of thermoregulatory function.

Introduction

In altricial chicks, food and heat are provided by the parents. Thus the development of the chicks is largely dependent on the behavior and the physiological constraints of their parents. In contrast, precocial chicks leave the nest shortly after hatching. They are self-feeding, and after hatching the role of the parents is limited to providing heat to the initially non-homeothermic chicks, keeping the family safe from predators and leading it to profitable feeding areas. The precocial mode of development implies that the chicks rather than their parents influence their own development through their behavior and physiological constraints. This has consequences for their survival and fitness.

The behavior of precocial chicks consists of foraging bouts during which they cool, alternated with brooding bouts during which they are re-warmed by a parent. Thus, the chicks are exposed to fluctuating weather conditions for a substantial amount of time, and their behavior is influenced by these weather conditions. Low ambient temperatures reduce the available foraging time of the chicks (Theberge & West 1973, Boggs *et al.* 1977, Beintema & Visser 1989b). In response to cold, their metabolism increases (Freeman 1993, Visser & Ricklefs 1993b, Marjoniemi & Hohtola 2000), body temperature decreases more rapidly (Ryser & Morrison 1954, Visser & Ricklefs 1993b) and to a lower level (Krijgsveld *et al.* 2003b; H Hötker *et al.* unpublished data), and digestive efficiency decreases (Kleiber & Dougherty 1934, Osbaldiston 1966). Little is known about the way in which the chicks allocate their resources when environmental conditions limit the availability of these resources. Precocial chicks need to invest in thermoregulatory and locomotory function, in addition to investment in growth. This presumably restricts their growth rate, relative to that of altricial chicks, through a trade-off between functional capacity and growth rate (Dawson & Evans 1957, Ricklefs 1979, Konarzewski 1988, Ricklefs *et al.* 1994, Starck & Ricklefs 1998). When the availability of resources becomes limited, for instance because a decrease in ambient temperature reduces the foraging time of the chicks, the balance between investment in growth on the one hand and thermoregulatory and locomotory function on the other hand may shift, as thermogenic function becomes more important. As a consequence, growth may be retarded or metabolic costs increase, which will affect the survival chances of the chick. The chick may be able to compensate for the reduction in resource availability by adjusting its behavior, and thus reducing the effect of unfavorable conditions.

In this study we determined whether and how a precocial chick adjusts its behavior in order to cope with unfavorable ambient temperatures, and we determined the flexibility in the balance between investment in growth and thermoregulatory function. We experimentally exposed chicks of Japanese quail (*Coturnix c. japonica*) to either high or low ambient temperatures. We determined how the foraging and brooding behavior of the chicks changed in response to ambient temperatures. In addition, we assessed changes in body temperature of the chicks during and at the end of foraging bouts, and we measured their food intake, metabolism and growth rate. Thus, we could determine how precocial chicks respond behaviorally and physiologically to low ambient temperatures and the consequent reduced foraging time.

Methods

Birds and housing

Newly hatched chicks (day 0) of Japanese quail from a fast growing strain bred for meat production were obtained from a commercial quail farm (de Kempische Kwartel, Lommel, Belgium) in 1999 and 2000. Birds were kept in wooden cages (l×w×h: 67×39×44 cm) under a light regime of 23L:1D (lights on 01:00 h) during the first 6 days to maximize survival chances of the chicks, and of 18L:6D (lights on 8:00 h) from day 6 onward. At one end of each cage a 60 W infrared heating lamp was placed. Food and water were provided *ad lib* at the opposite end. This design mimicked the options available to chicks in the field: they can either warm up being brooded by a parent without access to food, or cool down while foraging. Food consisted of Gallus 1 starter mix until 6 d of age, and of Gallus 2 food pellets (Kasper Faunafood, Woerden, Netherlands) from 6 d onward. Chicks were placed in subgroups of three per cage, since housing in smaller numbers causes distress. To address different questions, the experiments were carried out in 3 separate batches (experiment 1, 2 and 3), using the same design. In each experiment, two groups of 18 chicks were created randomly and placed in two rooms where a different temperature was maintained. The groups were both housed in 6 cages, each containing 3 birds.

In the first room, chicks were continuously exposed to temperatures of 24°C (range 22–25°C, room temperature) and in the second room chicks were continuously exposed to 7°C (range 6-8°C, minimum temperature that could be obtained). These two groups will subsequently be referred to as ’warm’ and ’cold’. The two temperatures reflect ambient conditions which foraging chicks may face under natural conditions: the warm temperature corresponds with moderate temperatures, the cold temperature corresponds with more extreme cold conditions.

To measure foraging behavior, body temperature and metabolic rates, chicks were taken out of their cages temporarily, whereas food intake was measured while chicks were under standard housing conditions (further details of measurements given below). It was possible to measure more than one of these variables during one experiment, because measurements lasted 24 h at most, did not involve all chicks simultaneousy, and were repeated every other day at most. Thus, in experiment 1 foraging behavior was measured alternately with metabolic rates. In experiment 2 foraging behavior was measured alternately with body temperature. In experiment 3 food intake was measured alternately with metabolic rates. Experiments were carried out under license of the University of Groningen (DEC nos. 2092 and 2322).

Behavioral observations

To study the foraging behavior of the quail chicks, 3 chicks from 1 cage were put together into an observation cage, which was a rectangular construction sized (l×w×h:) 2.5×0.5×0.5 m, made of fine-meshed (1 cm^2) hardware cloth with a wooden floor. At one end a brooding section of 30 cm wide was closed off with a wooden panel in which an entrance of 15×15 cm was cut out. A 60W infrared heating lamp was fitted in this section to create an area where the chicks could rewarm. At the opposite end of the cage, food was scattered on the floor and covered with a thin layer of wood shavings, to stimulate the chicks to spend time foraging. Food intake was not measured during these trials. Water was provided *ad lib*, but only in the foraging section. Observation cages were exposed to temperatures of either 24°C or 7°C, similar to standard housing conditions. Chicks were habituated to the observation cage for four hours at one and two days of age. Chicks were placed in the observation cage at least 4 h before the observation. Foraging experiments lasted 3 (experiment 1) or 4 hours (experiment 2). They were repeated at ages of 3, 7, 10, 14, 17, 23 and 30 days. In both warm and cold exposed chicks, behavior was measured in 8 subgroups of 3 chicks at each age (exceptions: 7 subgroups at 3 d; 4 subgroups at 17 and 23 d).

Behavior was classified as either warming, when the chick was in the brooding section, or cooling, when it was outside this section. Under cooling behavior, 3 behaviors were distinguished: foraging, resting, and other (*i.e.*, preening, standing or jumping). Huddling did not occur during foraging in the cold group and only sporadically in older chicks in the warm group. Behavior alternated between brooding bouts and cooling bouts. Behavior was recorded every 2 minutes for each chick. Behavior of the three chicks placed together in an observation cage was often highly synchronized (fig. 7.1). The analysis was therefore based on 3-chick averages as the independent data points.

Body temperature

In experiment 1, cooling bouts of chicks raised under cold conditions lasted 7 min on average, regardless of age. Based on these data, we set up a protocol in experiment 2 to measure the mean rate of decrease in body temperature (T_b), and to determine T_b at which the chicks returned to the brooder to be rewarmed. For each session, three chicks were placed together in an observation cage and were forced to alternately remain in the brooding section of this cage for 15 min or in the foraging section for 7 min. During each warming or cooling bout, T_b of each chick was measured once, after variable time intervals. For this purpose a thin thermocouple wire, attached to a digital thermometer (Omega, Laval, Canada; accuracy 0.1°C), was inserted 1 cm (small chicks) to 2 cm into the cloaca. This procedure was repeated until T_b's were measured for each chick after 1, 2, 4, 6 and 7 min of cooling, and after 1, 2, 4, 6, 8, 10 and 15 minutes of warming, in 6 cold and 6 warm chicks. In addition, some T_b's were taken beyond 7 min of cooling or 15 min of brooding, to obtain an extended T_b pattern. The measurements were performed at various ages. Analyses are based on individual data.

Observations on foraging behavior (see 'behavioral observations') were extended in experiment 2 on birds that were not in body temperature-trials. This extension of measurements resulted in a change in average cooling bout length of cold-raised chicks from 7 to 5 min (see results).

Food intake

In experiment 3, food intake was measured throughout development, at ages of 2, 9, 15, 23, 30, 37, 44, 51 and 57 days, by weighing the feeding trays at the beginning and end of a 24 h period, starting at ca. 0900 h, of 6 cages under cold and 6 cages under warm conditions. Spilled food that was scattered around by the chicks was collected and included in the weight of the left-over food. The mass of food ingested by three chicks could be deduced from the

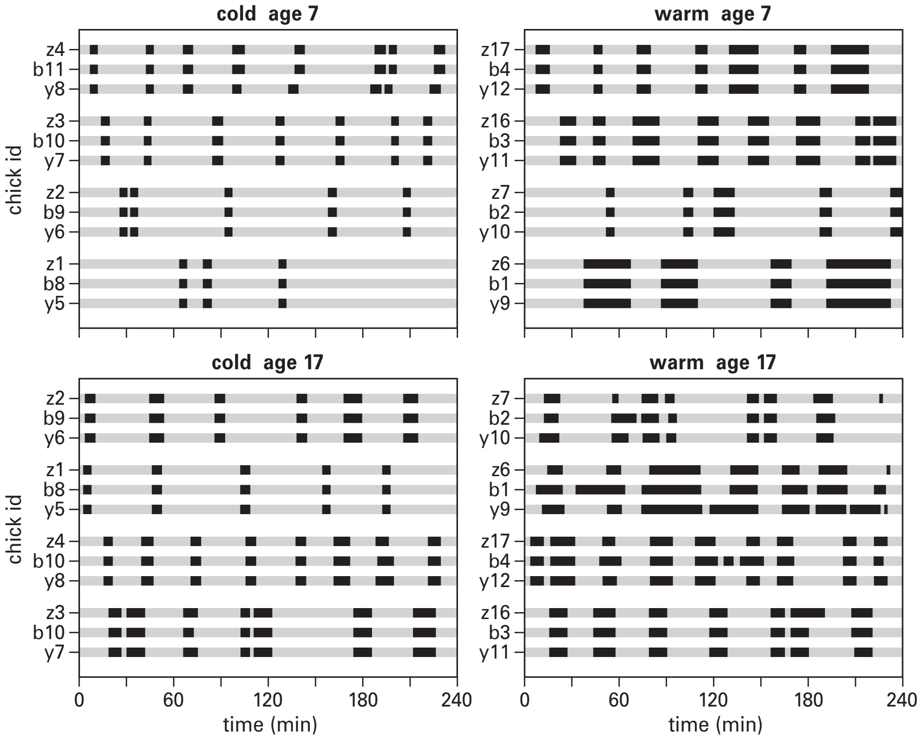

Figure 7.1. Cooling and brooding pattern of cold chicks (exposed to 7°C) and warm chicks (exposed to 24°C) of 7 and 17 days old. Each panel shows the actograms of 12 indiviual chicks which were housed in groups of three (clustered lines). Cooling bouts are shown as black bars, brooding bouts as light grey bars.

difference in weight of food before and after the experiment. Energy intake was calculated as the amount of food consumed H caloric content of the food (Gallus 1: 11.67 kJ g^{-1}; Gallus 2: 12.24 kJ g^{-1}).

Metabolic rate

Resting metabolic rates (RMR) and metabolic rates at 5°C and 20°C (temperatures chosen in respect of repeatability and comparability) of chicks of 7–8, 15–16 and 29-30 days of age (n = 6 at each age) were assessed during experiments 1 and 3 by measuring oxygen consumption in an open air flow system. Birds were placed individually in respiration boxes of 2 to 20 l without access to water or food, which were placed in dark, temperature regulated chambers. Oxygen consumption was measured simultaneously in six birds. Measurements lasted 5 to 7.5 h and were performed during daytime. Body mass and T_b were recorded at the start and end of the measurements.

Oxygen consumption was measured as follows (see also Boon *et al.* 2000): Dry air was pumped through the metabolic boxes at rates varying with age (from 20 l h^{-1} at 8 days to 60 l h^{-1} at 30 days of age) to obtain a difference between the in- and out flowing air of 0.5% oxygen or more. Flow rate was measured on the inlet air with a mass-flow controller (type 5850S Brooks) with an accuracy of 1%. The excurrent air was dried over molecular sieves (3 Å, Merck). Oxygen concentration in the in - and out flowing air was measured by a paramagnetic oxide sensor (Servomex Xentra 4100 gas analyzer), and carbon dioxide concentration by an infrared gas analyzer (Servomex 1440 gas analyzer), both with an accuracy of 0.01%. The oxygen and carbon dioxide analyzers were calibrated at regular time intervals with certified gas standards. The system recorded the oxygen and carbon dioxide differentials between dried reference air and dried air from the metabolic box. Six channels were employed simultaneously, using valves to switch between the channels once per minute (washout time 45 s). Including two reference channels, values were thus recorded with 8-minute intervals. Oxygen consumption was computed using equation 6 from Hill (1972), in which the gas data were corrected for changes in gas volume resulting from the carbon dioxide production with the use of the respiratory quotient. The obtained values were converted to energy expenditure (kJ h^{-1}) by applying an energy equivalent of 20 kJ l^{-1} O_2 (Gessaman & Nagy 1988).

At the start of the measurement ambient temperature, measured within the respiration boxes, was held at 30–33°C, to obtain a measurement of RMR, which was calculated as the lowest value of a 24-min running mean. After ca. 2 h, ambient temperature was then brought down by ca. 0.2°C per min (resulting in body cooling and in a gradual increase of MR) to either 5°C or 20°C, and metabolic rate at this temperature was recorded (average value calculated over a 24-min running mean). A peak level of metabolic rate was often reached in a chick before temperature had reached the minimum level of 5°C. Subsequently metabolic rate would decrease and the chick would cool down quickly. When such a peak and subsequent decline in metabolic rate was observed, the measurement was terminated and the value of peak metabolic rate was used instead of the value at 5°C.

Growth

Body mass was recorded every day or every other day in the morning in each chick until 35 days of age. Wing chord length, tarsus length and head-bill length (maximum length from the tip of the bill to the back of the head) were measured in each chick every three days. Beyond the age of 35 days, measurements were continued in 6 cold and 6 warm chicks; body mass measurements every other day and the other measurements once per week. Estimates of growth parameters were obtained by non-linear curve-fitting of the Gompertz' equation.

Statistical analysis

Data were analyzed statistically using SPSS version 7.5 (SPSS Inc., Chicago, 1997). When data were normally distributed, Independent samples *T*-test) were used to analyze differences between the warm and cold-raised group. For non-parametric analysis of more than two groups, Friedman's test was used (food intake). General linear models (GLM) were used to test differences in boutlength and percentage foraging time as well as metabolic rates, where metabolic rate and body mass were log-transformed. Percentages were arc-sine transformed before analysis.

Results

Behavior pattern

The behavior pattern of the quail chicks consisted of alternating bouts of cooling and warming, as illustrated in figure 7.1. From these data, the duration and number of cooling and warming bouts was determined, as well as the total amount of time spent cooling. Cooling bouts were shorter in cold (7°C) than in warm (24°C) chicks (fig. 7.2A; Independent samples *t*-test, $t = 4.4$, df = 41, $P < 0.001$). At 24°C cooling bout length increased with age from 10 to ca. 30 min, whereas in the cold cooling bout length was 5 min on average, and did not change with age (general linear model (GLM); effect of age ($F_{1,\,90} = 5.6$, $P < 0.05$) and effect of the age × rearing temperature interaction ($F_{1,\,90} = 27.1$, $P < 0.001$); overall model

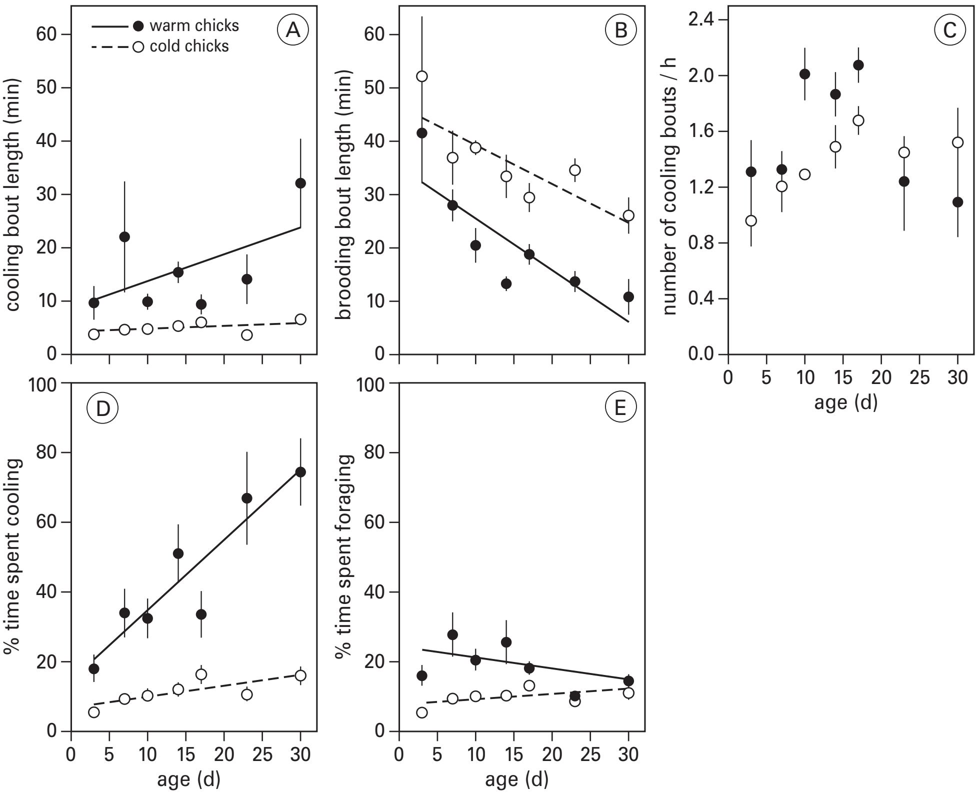

Figure 7.2. Behavior of cold-exposed and warm chicks as a function of age. Shown are the average lengths of the cooling (A) and brooding (B) bouts; the number of cooling (and brooding) bouts per hour (C); the time that is spent on cooling behavior as a percentage of the total time available (D); and the time that is spent on foraging as a percentage of the total time available (E). Averages are shown ± se.

$F_{2,\,90} = 15.7$, $P < 0.001$, $r^2 = 0.26$). Brooding bouts were longer in cold chicks than in warm chicks (fig. 7.2B) and brooding bout length decreased with age in both warm and cold chicks (GLM; effect of age ($F_{1,\,91} = 30.1$, $P < 0.001$) and of rearing temperature ($F_{1,\,91} = 30.0$, $P < 0.001$), no interaction; overall model $F_{2,\,91} = 28.8$, $P < 0.001$, $r^2 = 0.39$). The number of cooling bouts per hour was lower (and thus the total cycle length longer) in the cold than in the warm group up to an age of 17 days, and increased up to this age in both groups (fig. 7.2C; GLM; effect of age ($F_{1,\,70} = 24.8$, $P < 0.001$) and of rearing temperature ($F_{1,\,70} = 14.4$, $P < 0.001$), no interaction; overall model $F_{2,\,70} = 17.9$, $P < 0.001$, $r^2 = 0.34$). After this, the number of bouts decreased strongly in the warm group, to a level below that of the cold group. With increasing age, the start and end of cooling bouts remained more synchronized in cold than in warm chicks (see fig. 7.1).

This pattern of behavior resulted in cold chicks spending a smaller percentage of time on cooling behavior than warm chicks (fig. 7.2D). Cold chicks initially spent only 5% of the available time cooling, which increased with age to 16% at 30 days. In warm chicks, cooling behavior started out at 18% of the available time and increased to 74% (GLM; effect of age ($F_{1,\,94} = 48.2$, $P < 0.001$), of rearing temperature ($F_{1, 94} = 4.2$, $P < 0.05$), and of the age × rearing temperature interaction ($F_{1, 94} = 19.5$, $P < 0.001$); overall model $F_{3, 94} = 62.8$, $P < 0.001$, $r^2 = 0.67$, data arcsine-transformed).

Initially, cold chicks were continuously foraging during cooling. However, as chicks grew older they spent more time resting or preening, reducing the time spent foraging to 70% of the total cooling time. In warm chicks, behavior other than foraging started at an earlier age and reached higher percentages as they grew older than in cold chicks (fig. 7.3). The resulting time spent on foraging alone was only 5% of the total time for three-day old cold chicks. As the chicks grew older this percentage increased to 11% at 30 days old, but values remained low. Warm chicks spent more time on foraging, ca. 20% initially, and this percentage decreased as they grew older to levels close to those of the cold chicks (fig. 7.2E).

Body temperature

During cooling, T_b decreased faster at low (7°C) than at high (24°C) temperature, and decreased faster in younger than in older chicks (fig. 7.4). In chicks exposed to low temperatures, the T_b at which the chicks returned to the brooder ranged from 37.8°C (sd = 0.51, n = 5) on average in 3 day old chicks to 41.0°C (sd = 0.28, n = 6) on average in 15 day old chicks. In chicks exposed to high temperatures this minimum T_b was higher, averages ranging from 40.1°C (sd = 0.50, n = 6) in 3 day old chicks to 41.9°C (sd = 0.38, n = 6) in 15 day old chicks. At all ages and in both cold - and warm-exposed chicks, T_b returned to levels of 40.5–41°C within the average duration of a brooding bout.

Food intake

Daily food intake increased until the chicks were 30 days old (*i.e.*, body mass ca. 200 g), and thereafter leveled off (fig. 7.5, upper panel). Up to 15 days of age (ca. 100 g), daily food intake was similar in the cold and warm group. After that, cold chicks had a higher food intake (independent samples *T*-test: $T = 5.6$, df = 35, $P < 0.001$). However, since cold-exposed chicks initially had a lower body mass, they consumed 15% more food per gram body mass than the chicks exposed to high temperatures. As body mass of cold-exposed chicks over 20 days of age was higher than that of warm chicks, mass-specific food of cold-exposed chicks remained 15% higher than that of warm chicks, rather than increasing further (Friedman's test: $\chi^2 = 9.0$, n = 9, $P < 0.005$). The level of mass-specific food intake decreased from 0.28 g food per g body mass on average at 10 days of age to 0.12 on average at 37 days and older. Foraging

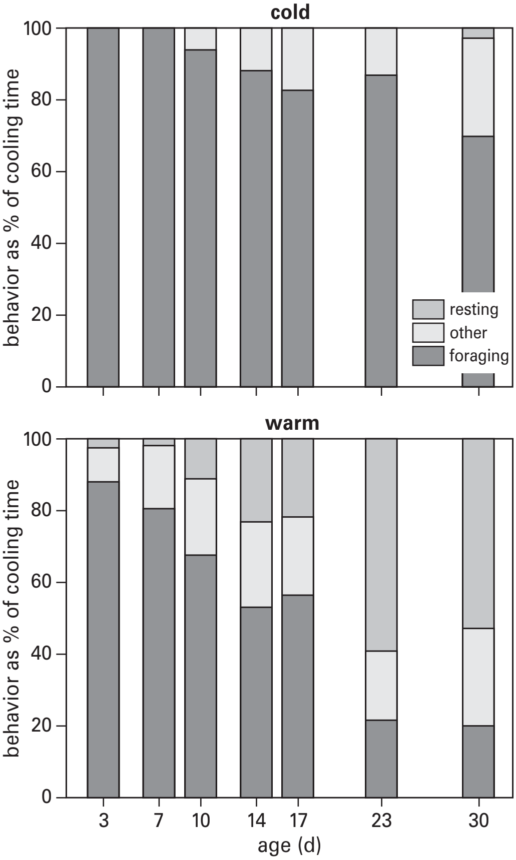

Figure 7.3. Percentage of cooling time that chicks spent on either Foraging, Resting, or Other behavior (e.g., preening, running, jumping). The two panels show the difference between cold-exposed and warm chicks.

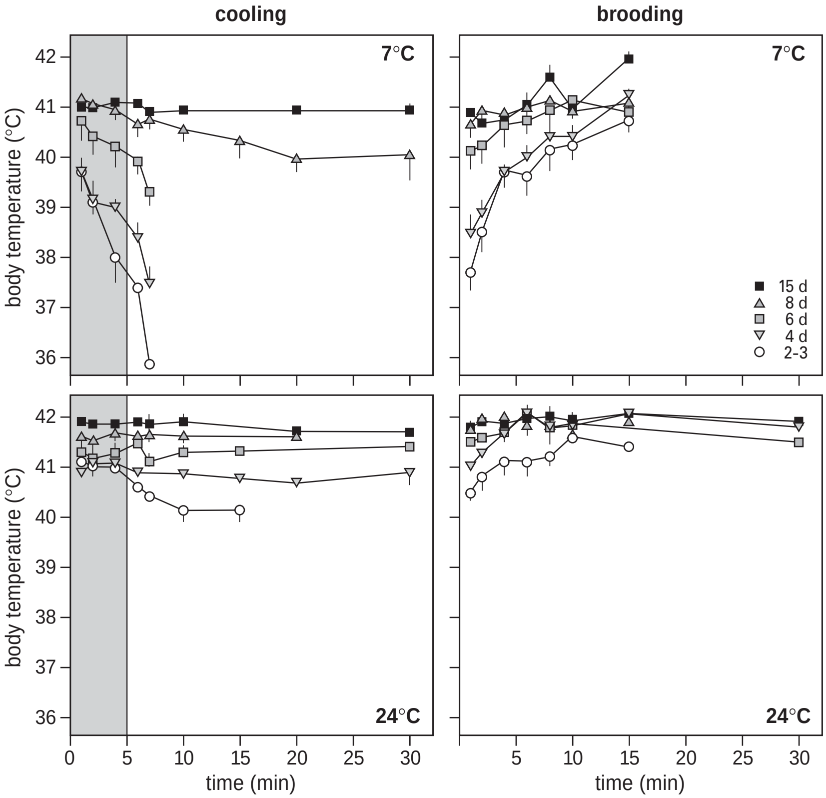

Figure 7.4. Body temperatures (mean ± se) of chicks of various ages, during cooling (right panels) and subsequent rewarming (left panels) sessions, plotted as a function of exposure time. Upper panels: Chicks exposed to 7°C. Lower panels: Chicks exposed to 24°C. Each datapoint represents the average value of 6 chicks. The vertical line at 5 min indicates the average time at which cold chicks ended a cooling bout.

efficiency (roughly measured as mean food intake divided by the number of hours spent on foraging; fig. 7.5, lower panel) increased almost linearly with age and was higher in cold-exposed than in warm chicks. Initially, it was 3.4 times higher, but this difference decreased with age to 1.5 at 30 days of age.

Metabolic rate

Resting metabolic rates (RMR) and metabolic rates at 5°C and at 20°C (fig. 7.6) did not differ significantly between cold and warm chicks of 8 days old when taking into account the smaller body mass of cold-raised chicks at this age. However, the increase in metabolic rate with age was more rapid in cold-exposed chicks, which resulted in higher levels of metabolism in these chicks than in warm chicks when they were older than 8 days (GLM: log(RMR): effect of log(body mass) ($F_{1,\,33} = 403.2$, $P < 0.001$) and of the log(body mass) × rearing temperature interaction ($F_{1,\,33} = 7.1$, $P < 0.05$); $F_{2,\,33} = 203.1$, $P < 0.001$, $r^2 = 0.95$). GLM: log(MR at 5°C): effect of log(body mass) ($F_{1,\,32} = 280.5$, $P < 0.001$), of rearing temperature ($F_{1,\,32} = 12.0$, $P < 0.005$) and the log(body mass) × rearing temperature interaction ($F_{1,\,32} = 4.1$, $P < 0.005$); overall model $F_{3,\,32} = 118.3$, $P < 0.001$, $r^2 = 0.92$). The effect of age was explained entirely by body mass.

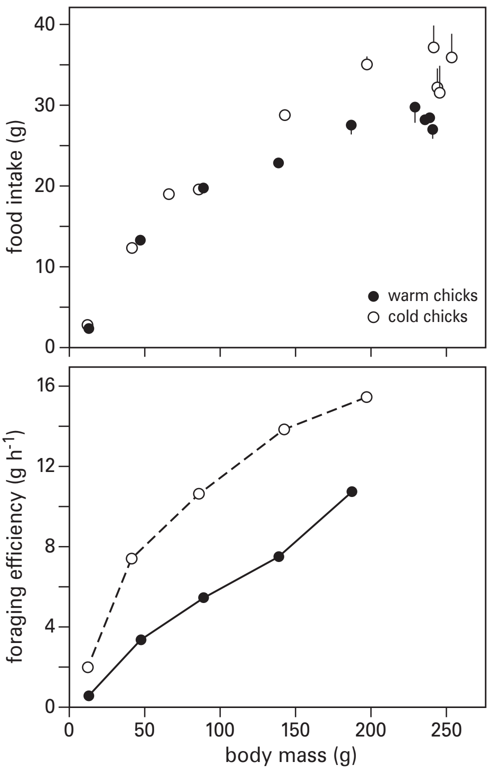

Figure 7.5. Daily food intake (24 h, upper panel; mean ± se) and foraging efficiency (lower panel; food intake / h spent on actual foraging) of cold-exposed and warm chicks in relation to age.

The development of mass-specific metabolism followed the same pattern as whole body metabolism, with the decrease in mass-specific metabolism being more pronounced in warm chicks, resulting in higher levels of mass-specific metabolic rates in cold than in warm chicks at higher body masses (GLM: log(mass-specific RMR): effect of log (body mass) and of the log(body mass) × rearing temperature interaction; overall model $F_{2,\,33} = 24.4$, $P < 0.001$, $r^2 = 0.60$. GLM: log(mass-specific MR at 5°C): effect of log (body mass) and of the log(body mass) × rearing temperature interaction; overall model $F_{2,\,33} = 60.8$, $P < 0.001$, $r^2 = 0.79$).

From the metabolic rates during foraging, as well as the metabolic rates during brooding (RMR), we estimated how much a chick's metabolism was reduced when it returns to the brooder instead of continuing to forage. Metabolic reductions were highest in 8-day old cold chicks, which reduced their metabolism by 60%. This reduction decreased to 48 and 50% at 16 and 30 days respectively. In warm chicks the metabolic reduction was smaller and did not change with age; their metabolism was reduced by 37, 36 and 37% respectively at 8, 16 and 30 days of age.

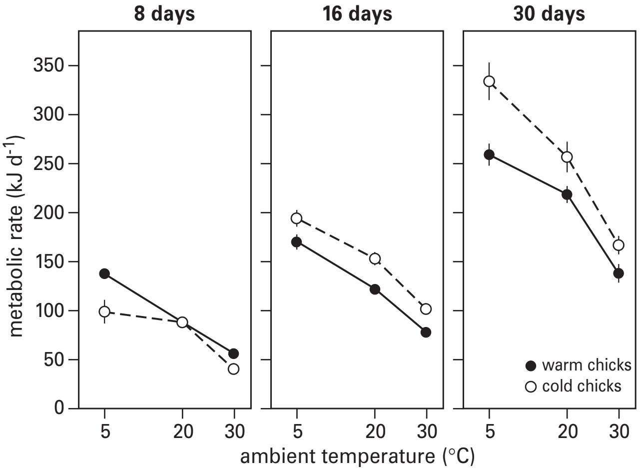

Figure 7.6. Metabolic rates of cold-exposed and warm chicks at thermoneutral temperature (RMR), at 20°C and at 5°C, at different ages. Averages are shown ± se.

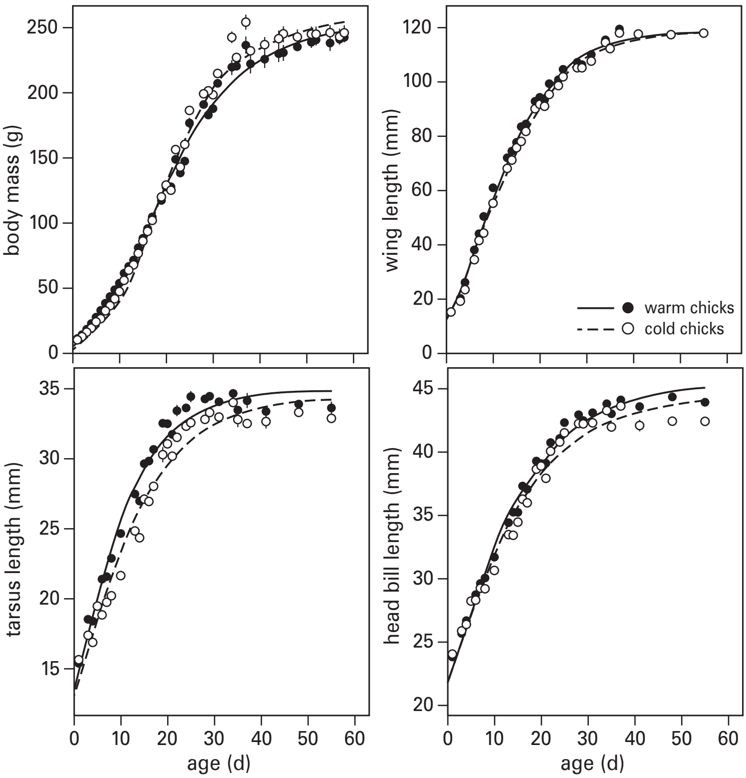

Figure 7.7. Development of body mass, wing length, tarsus length and head bill length up to 58 days of age, for chicks raised under cold and warm conditions. Daily averages are shown with standard errors. The lines denote the average growth curves obtained by nonlinear curve-fitting of the Gompertz' equation.

Growth rate

Growth of the cold and warm chicks did not show large differences. However, growth of cold chicks initially was retarded compared to warm chicks (fig. 7.7). Around 14 days of age, body mass of the two groups was similar, and at ca. 20 days of age, body mass of the cold chicks exceeded that of the warm chicks. Wing, tarsus and head-bill length were smaller in the cold group at all ages, although the difference in wing and tarsus length became smaller as the chicks matured. By calculating the weekly increase in body mass and size of the chicks, we determined that the reduced growth rate in cold chicks occurred only in chicks up to one week old (fig. 7.8; Independent samples *t*-test: mass: $t_{114} = 6.9$, $P < 0.001$; wing: $t_{113} = 5.2$, $P < 0.001$; tarsus: $t_{113} = 11.4$, $P < 0.001$; head bill: $t_{114} = 3.7$, $P < 0.001$). From 7 to 14 days of age, growth was similar for mass and wing length, but growth of tarsus and head bill was still reduced in cold chicks (indep. samples *t*-test: mass: $P > 0.05$; wing: $P > 0.05$; tarsus: $t_{112} = 2.3$, $P < 0.05$; head bill: $t_{112} = 3.7$; $P < 0.001$). In cold chicks between 14 and 28 days of age, increase in mass exceeded that of warm chicks (indep. samples *t*-test: mass at 21 days: $t_{108} = -4.0$, $P < 0.001$; mass at 28 days: $t_{108} = -4.4$, $P < 0.001$) and in chicks older than 28 days the differences between the two groups disappeared. Increase in size followed a pattern more or less similar to that of mass, but the

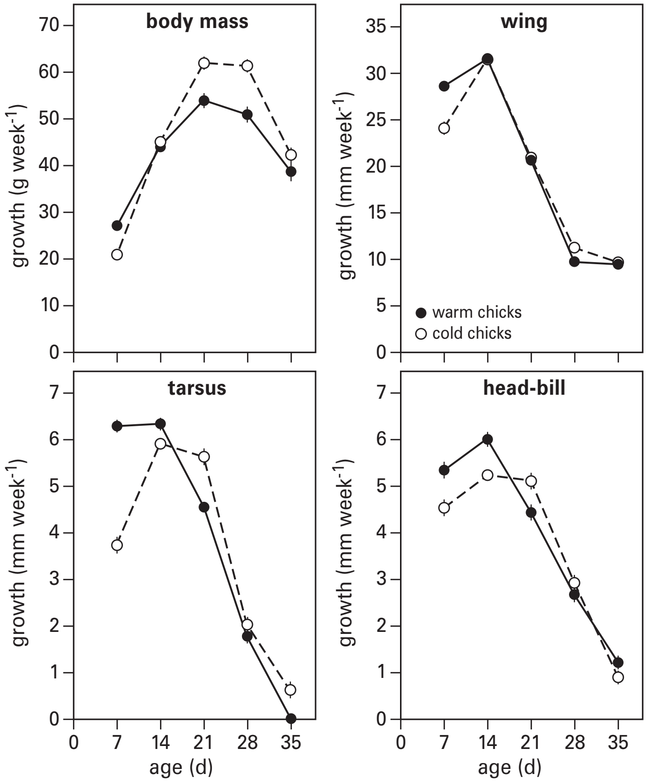

Figure 7.8. Growth rate of cold-exposed and warm chicks, calculated as the increase per week in body mass, wing length, tarsus length and head bill length. Weekly averages are shown ± se.

differences in growth rate between cold and warm chicks of ages older than 14 days did not become as large as those for body mass.

Discussion

Foraging time

Quail chicks raised in the cold shortened their foraging bouts and lengthened their brooding bouts compared to chicks in higher ambient temperatures. This is energetically beneficial, since exposure to cold involves higher metabolic costs. In addition, digestive rate may be higher at higher body temperatures. A reduction in foraging bout length as ambient temperature decreases has been observed in chicks of willow ptarmigan (*Lagopus lagopus*, Pedersen & Steen 1979), and for free-living chicks of American golden plover (*Pluvialis dominica*, Krijgsveld *et al.* 2003b). As a result of the shortened bout lengths in combination with a lowered alternation of cooling and brooding bouts, the total cooling time was strongly reduced under cold conditions, as is known also in other precocial species (Boggs *et al.* 1977, Beintema & Visser 1989b; H Schekkerman *et al.*, unpublished data).

Body temperature

The proximate cause to terminate a cooling bout has long been thought to lie in the body temperature of the chick (Pedersen & Steen 1979, Chappell 1980): Since a young chick cools during foraging, it will eventually reach a critical minimum body temperature, below which for instance locomotion becomes more sluggish, which will limit foraging bout length. However, our data show that quail chicks stop foraging before this critical temperature is reached. In our quail chicks exposed to 7°C, body temperature dropped to lower levels than in chicks exposed to 24°C. At three days of age, mean minimum body temperature at which chicks ended their foraging bout was 37.8°C in cold chicks versus 40.1°C in warm chicks. The warm chicks still showed a regular pattern of brooding and cooling bouts, despite the fact that, unlike the cold-exposed chicks, they hardly cooled down. Also, in chicks of avocet (*Recurvirostra avosetta*) and American golden plover, mean body temperature at the end of a foraging bout was lower at low than at high ambient temperatures (Krijgsveld *et al.* 2003b; H Hötker, unpublished data). In addition, in both quail and American golden plover chicks, brooding still occurred beyond the age at which the chicks are able to thermoregulate (Krijgsveld *et al.* 2003b). Given these results, it is unlikely that body temperature alone determines the length of a foraging bout.

Energetic considerations can explain the foraging behavior of the chicks to a considerable extent. The metabolic rate (including RMR) of cold chicks of 8 days old was equal to or lower than that of warm chicks, whereas at older ages cold chicks had higher metabolic rates. In addition, the reduction in their metabolic rate when switching from foraging to brooding was considerably higher than in warm chicks. Thus, in contrast to warm chicks, cold chicks would experience a net loss of energy when they would continue cold exposure longer than strictly necessary. By increasing their foraging efficiency, they could reduce the time needed for foraging, and spend more time in the brooder. Under conditions where food availability is a more limiting factor, it will be more difficult to increase foraging efficiency. In that case chicks will be forced to continue foraging until their requirement is met, or until some other factor, like impaired digestion or low T_b restricts foraging time. Eventually limited foraging time will lead to constrained energy acquisition, which may lead to a stronger reduction of thermoregulatory function and growth rate (van der Ziel & Visser 2001).

Food intake

Mass-specific food intake was higher in cold-exposed than in warm chicks at all ages, a similar response as has been shown in other animals (Toloza *et al.* 1991, Konarzewski & Diamond 1994, McWilliams & Karasov 1998). Cold chicks achieved this increase despite the small percentage of time that they spent on foraging, by increasing their foraging efficiency compared to that of warm chicks. It remains unknown whether this occurred through an increase in storage capacity or throughput capacity of the gut.

Apparently the increase in food intake was initially not sufficient to sustain growth, as body size was lower than that of warm chicks during the first 3 weeks of age. Since food was available *ad lib* when chicks were not in a time budget experiment, limited foraging time cannot be the cause for this. Physiological constraints on either metabolism or food intake are more likely to have limited the intake (Harun *et al.* 1997, Jørgensen & Blix 2000, McWorther & Martínez del Rio 2000, Yahav 2002; Y Zharikov *et al.*, unpublished data).

Thermoregulatory capacity versus growth

Exposure to low temperature did not have severe or lasting effects on the morphology or physiology of the chicks, except for the head-bill length, owing to an almost complete catch-up growth later in development. Apparently, developmental plasticity is high in precocial quail chicks. High plasticity will be of great importance for the development and survival of precocial chicks, which often have to deal with adverse weather conditions, in contrast to altricial species which show a more limited ability to adjust their growth rates (Konarzewski 1988, Schew & Ricklefs 1998).

The elevated RMR in cold chicks may indicate an increase in their thermogenic capacity relative to that of warm chicks. An elevated RMR is associated with a permanent extra cost, by which increases in energy supplying organs are supported (Hammond & Diamond 1997). Since the skeletal muscles are the main source of heat generation (Dawson 1975, Hohtola & Stevens 1986), and the capacity of the chick to produce heat increases as the size and maturity of these muscles increase (Ricklefs 1983, Choi *et al.* 1993, Krijgsveld *et al.* 2001), a rise in the thermogenic capacity of the chick would coincide with an increase in its RMR.

In addition, as a consequence of cold-exposure and limited food-processing capacity, investment in growth was reduced to a further extent than investment in thermoregulatory capacities. This is shown by the lag in the increase of growth rate compared to the increase in RMR in cold chicks: at 8 days of age, RMR in both groups was similar whereas growth rate was lower in cold chicks; at 15 days of age RMR was higher in cold chicks and growth was similar in both groups; and at 21 days of age, both growth rate and RMR were higher in cold chicks. Once food intake increased, at 23 days of age, growth rate of the cold chicks increased as well, which reversed the difference in body mass between the two groups. Similar results were found by (Yahav 2002) and (Marjoniemi & Hohtola 2000). The results suggest that the balance between investment in growth on the one hand and thermoregulatory (and locomotory) function on the other hand shifted in the favor of thermoregulatory function and at the cost of growth when precocial chicks are exposed to cold.

Acknowledgements

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Chapter 8

Limits to low body temperature during foraging in precocial shorebird chicks

Karen L Krijgsveld, Simon Verhulst & Robert E Ricklefs

Abstract

Chicks of precocial species can lower their body temperatures considerably during foraging, from 39ºC down to 20–25ºC. Although this mechanism is highly adaptive for survival, the degree to which shorebird chicks exploit this option when foraging is poorly known. We measured body temperatures of shorebird chicks (Scolopacidae) foraging under semi-natural conditions. These chicks alternated bouts of foraging during which they cool, with bouts of passive rewarming under an artificial heat source. Foraging chicks maintained their body temperatures at a minimum of 36ºC. Chicks maintain high body temperatures under cold conditions by foraging for shorter periods more frequently rather than foraging for more extended but less frequent periods. We calculated that overall foraging time would decrease if chicks were to let their minimum body temperatures drop lower, because the time needed for passive rewarming increases disproportionately. We argue that as a consequence, lowering body temperature below ca. 35ºC is not beneficial to the foraging chick. Instead, by minimizing foraging bout length and increasing brooding time, and thus maintaining high body temperatures, chicks can considerably reduce energy expenditure, while simultaneously increasing the rate and efficiency of digestion.

Introduction

Body temperatures of young birds can fluctuate widely. While body temperatures of birds in thermoneutral conditions are typically 38-39°C, chicks of altricial species have been shown to cool to 20ºC when parents are off the nest (Weathers *et al.* 1990). During foraging, chicks of precocial species can cool to body temperatures as low as 25°C and still recover (Myhre & Steen 1979). At the extreme, Bunni (1959) reported a killdeer chick (*Charadrius vociferus*) recovering function after recording a cloacal temperature of 15ºC. For precocial chicks, this fluctuation in body temperature can be understood in an ecophysiological context. Chicks of shorebirds are self-feeding but cannot maintain their body temperatures when young (Nice 1962, Visser & Ricklefs 1993b). They therefore alternate bouts of foraging with bouts of rewarming under the parent. As the chicks age, their level of homeothermy increases and their foraging bouts become longer (Krijgsveld *et al.* 2003a,b). The rate of heat loss is dependent on the environmental conditions, resulting in longer foraging bouts when ambient temperatures are higher (Krijgsveld *et al.* 2003a,b). Especially on the arctic tundra, chicks are faced with highly variable environmental conditions, while at the same time the short arctic season demands rapid development.

Precocial chicks deal with low ambient temperatures and brief growing seasons through a number of physiological and behavioural adaptations. For example, daily energy expenditure and catabolic capacity are comparatively high (Visser 1993b, Krijgsveld *et al.* 2001 [chapter 4], Joest 2003, Schekkerman *et al.* 2003, Tjørve *et al.* 2007a, b, Krijgsveld *et al.* 2012 [chapter 5]), allowing high levels of thermoregulation and good locomotory capabilities. Growth rates however are reduced compared to altricial chicks, in favour of functional maturity (Starck & Ricklefs 1998), while simultaneously growth rates are highly flexible (Shea & Ricklefs 1996, van der Ziel & Visser 2001, Krijgsveld *et al.* 2003a [chapter 7]), enabling the chicks to slow development during adverse weather or food conditions. Time budgets, in particular the length of periods spent foraging and rewarming, are flexible (Sullivan Blanken & Nol 1998, Schekkerman 2008, Krijgsveld *et al.* 2003a,b). Finally, the range of body temperatures (T_b) within which chicks can be active is broad, allowing chicks to extend foraging bouts under cooling conditions

(Chappell 1980, Norton 1973, Myhre & Steen 1979, Pedersen & Steen 1979, Brown & Downs 2002, Krijgsveld *et al.* 2003a,b).

Although low body temperatures convey advantages to foraging precocial chicks, because they allow longer foraging bouts and increase survival during adverse conditions, they may be detrimental as well. For instance, as chicks cool, locomotory activity and foraging efficiency decrease (Kleiber & Dougherty 1934, Osbaldiston 1966, Norton 1973, Aulie 1976. Rojas 2012), and such effects decrease the benefits of extending foraging bout length in addition to increasing vulnerability to predators. Thus, chicks need to optimize foraging bout length, and it is an open question whether they exploit their ability to let their body temperatures fall to low levels or instead maintain body temperatures at higher levels during foraging.

To determine how much body temperatures fluctuate, we measured body temperatures of precocial chicks that were foraging and rewarming under semi-natural conditions. Measurements were done in five species of sandpipers ranging in neonatal mass from 4 to 33 g and thus ranging widely in homeothermic capacity.

Material & Methods

Study area, birds and housing

We studied, from the smallest to the largest species, least sandpiper (*Calidris minutilla*), dunlin (*Calidris alpina*), lesser yellowlegs (*Tringa flavipes*), Hudsonian godwit (*Limosa haemastica*), and whimbrel (*Numenius phaeopus*). Observations and measurements were performed from 1996 through 1998 on the subarctic tundra near Churchill, Manitoba, Canada (58°45'N, 94°04'W). Eggs were collected on the tundra in June and July and were incubated at 36.5–37.5°C, at a relative humidity of 55% until shells were star pipped (2–3 days before hatching), when it was increased to 85%. Hatching success was 80–90%, including eggs exhibiting no development and which may therefore have been infertile. The day of hatching was designated as chick age 0.

Chicks were kept for a minimum of one day in cardboard boxes (0.5×1 m) fitted with light bulbs to provide warmth and provided with *ad lib* food and water, in the laboratory, to allow them to dry and start feeding. For a detailed description of the housing conditions, see Krijgsveld *et al.* (2001). From an age of 2 days onward, chicks were placed in an outside enclosure in groups of two to eight chicks, which were used in simultaneous experiments. The enclosure was circular with a diameter of 10–15 m and was surrounded by a chicken-wire fence 50 cm high, lined along the lower 20 cm with cloth and plastic and fixed firmly to the ground with tent pegs to prevent escapes. An artificial brooder provided heat to the chicks. It consisted of a wooden box of 20 (height) × 30 (depth) × 20 (width) cm, with an entrance of 15 × 15 cm, in which a light bulb and a thermal blanket were placed, maintaining a temperature of up to 41°C closest to the light bulb. The light from the bulb served to direct chicks to the brooder. Chicks learned to enter the brooder to be rewarmed within two days. Chicks that had not yet learned to use the brooder effectively were excluded from analysis (e.g., chicks showing huddling behaviour and distress calls). Chicks were left in the enclosure for periods of 6 to 24 hours a day, depending on their capability to use the brooder. Because naturally available food diminished rapidly in the enclosure, food and water were supplied *ad lib* on a dish as well as scattered on the ground. Food consisted of turkey pre-starter mix (Puratone Corporation, Niverville, Manitoba, Canada), supplemented with a mix of tuna, chicken, oatmeal, and boiled eggs, as well as with defrosted mosquitoes caught in the area. Nutrients of the food were proportioned to resemble natural insect food.

After the observations and temperature measurements, chicks were either used for other experiments or were released in their natural environment when they had reached their fledging age. Observations and collection of eggs were carried out under permit from the Canadian Wildlife Service and husbandry and laboratory procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri–St. Louis.

Temperature transmitters

Temperature-sensitive transmitters (Holohil Systems Ltd. Carp, Ontario, Canada) were implanted in two whimbrel chicks to measure body temperature. Transmitters weighed 0.74 g (2.2% of neonatal body mass) and were 18×6×4 mm in size. Interval of the signal of the transmitters increased with increasing temperature (range 1200–2000 msec per 10 signals). Transmitters were calibrated by the manufacturer and again by us just before implantation. The two calibrations yielded very similar results and the latter was used to calculate body temperature. Transmitters were implanted in the body cavity of the chicks when they were one day old. For this purpose, birds were anesthesized with 0.5 ml/kg of a mixture of ketamine (25 mg/ml) and rompun (2 mg/ml) which was injected intramuscularly in the upper leg muscle (low in iliotibialis). An incision of ca. 1 cm was then made in the skin and through the subcutaneous layers, through which the transmitter was inserted into the abdominal cavity. The incision was closed with 1 or 2 sutures through all layers simultaneously, with the transmitter being attached to the suture material to allow easy removal of the transmitter after the experiment. The bird was then placed at 35°C to recover. The procedure took ca. 20 min from injection to finish. Birds woke up 30–40 min after injection. Behaviour and growth of the chicks did not deviate from similarly aged chicks without transmitters (data not shown). Transmitters were removed at 22 and 6 days of age respectively. Rechecking the calibration showed no change over the observation period.

Observations and temperature measurements

Foraging behaviour of whimbrel chicks fitted with transmitters was observed and T_b was measured from a blind adjacent to the enclosure. The two whimbrel chicks fitted with a transmitter were placed in the enclosure together with three to seven other chicks. All chicks were color-banded individually to allow individual recognition. Time budgets were determined by recording every minute whether chicks were foraging or brooding. During observations, T_b of the two chicks was recorded every minute by measuring the time interval of 10 signals.

Body temperature was measured rectally in chicks of all other species. To obtain measurements of rectal temperature, the observation protocol deviated slightly. Here, foraging behavior was observed and T_b was measured from within the enclosure, where the observer sat quietly on the ground. Chicks were not disturbed by the presence of an observer, and often approached to catch mosquitoes that were attracted by the observer. T_b was measured by quickly picking up the chick and inserting a greased, thin thermocouple wire (30 gauge, tip dipped in a drop of nail polish to cover the sharp end), attached to a digital thermometer (Omega, Laval, Canada; accuracy 0.18°C) 1 cm into the cloaca. Rectal temperature of whimbrel chicks was ca. 0.5°C lower than core body temperature as measured with the transmitters, but otherwise accurately reflected changes in T_b. T_b was not measured more than once every half-hour per chick. Body temperatures were not measured during brooding, to avoid influencing length of brooding bouts. After a T_b-measurement, behavior of the chick was not recorded for 5 min to allow the chick to return to a routine. Behavior of the chicks was not noticeably affected by the measurement (comparison of behaviors from chicks that were and were not picked up for temperature measurements).

Environmental conditions

Ambient temperature and wind speed were measured continuously, at 10 cm above the ground. Ambient temperature was measured with two 3.5-cm spheres, one white and one

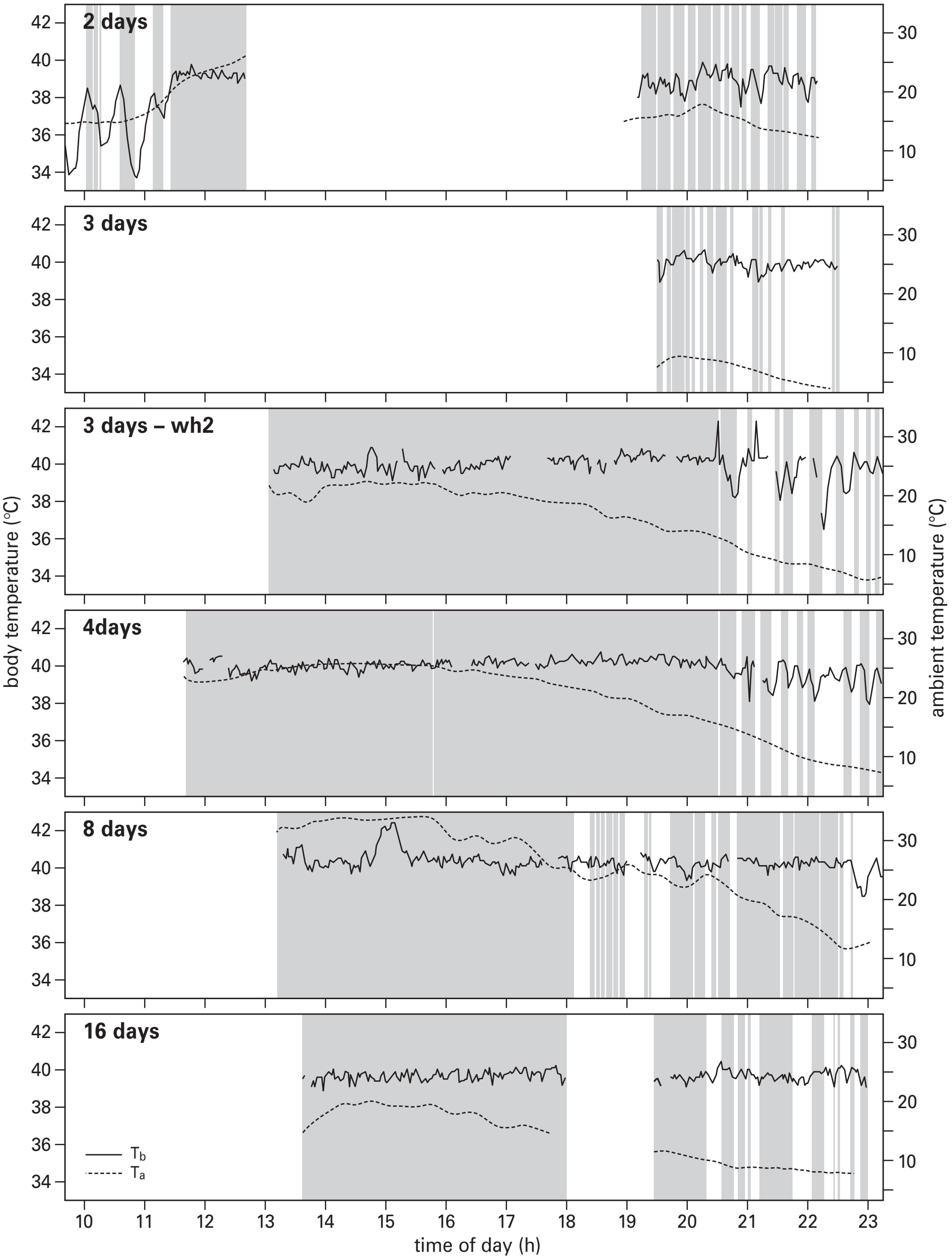

Figure 8.1. Body temperatures of two whimbrel chicks during foraging and brooding bouts in an enclosure, as measured with temperature-sensitive transmitters impanted in the body cavity. All panels show data for the same individual whimbrel chick at different ages, except for the third panel from the top which shows data for a second whimbrel chick at three days of age. Body temperature is shown as a solid line, ambient temperature as a dashed line. Brooding bouts are indicated as grey bars, foraging bouts are shown in white when data for T_b and T_a are given.

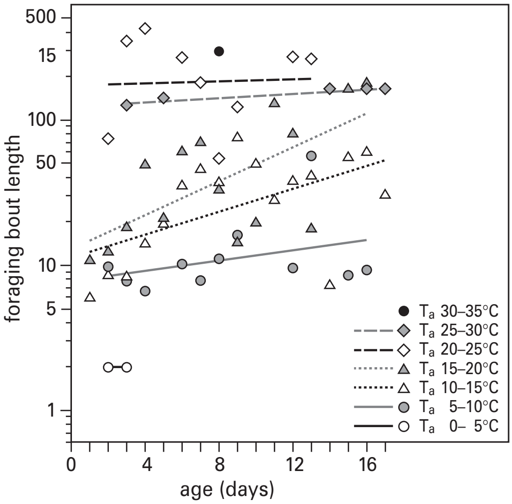

Figure 8.2. Foraging bout lengths of whimbrel chicks under semi-natural foraging conditions, showing a general increase in bout length with age and with ambient temperature. Bout lengths are averaged per age and per temperature class, with a minimum of 1 and a maximum of 26 values per average. Linear regressions are fitted to lead the eye. Note log-scale on Y-axis.

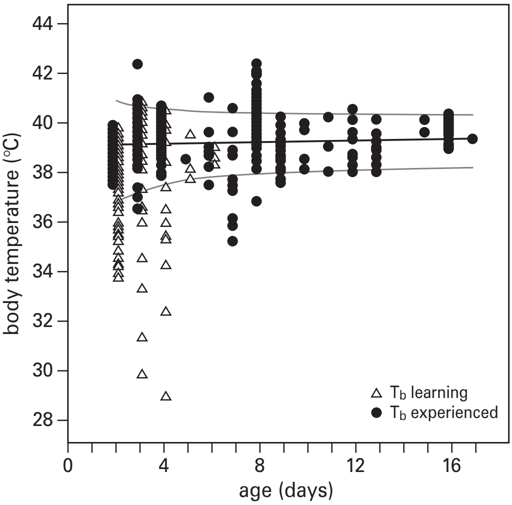

Figure 8.3. Body temperatures of whimbrel chicks in relation to age. Temperatures measured both rectally and internally. Body temperature of chicks that were still learning to find the brooder (grey triangles) dropped considerably more than that of experienced chicks (black circles). Lines depict the regressions of minimum, maximum (grey lines, fitted with inverse function) and mean (solid line; linear function) temperatures.

black, both with internally mounted thermocouples. Wind speed was measured with a cup anemometer (A100L2, Grant Instruments Ltd., Barrington, UK). The climate data were averaged over intervals of 15 min and recorded with a Squirrel 1204 data-logger (Grant Instruments Ltd.). For details see Krijgsveld *et al.* (2003b). In addition, data on wind speed, ambient temperature and radiation measured at 10 m above ground were obtained from the local airport, at ca. 20 km distance.

Results

Core body temperature of foraging whimbrel chicks

T_b of the two whimbrel chicks with implanted temperature-transmitters was followed during foraging and brooding bouts in the enclosure. When first introduced to the enclosure, during the first two hours the first chick (2 days old) showed relatively long foraging bouts and dropped its T_b to 34-36°C (minimum 33.7°C; fig. 8.1 upper panel). T_a then increased and the chick foraged continuously for an hour at a T_b of ca. 39°C. At the end of the day, T_a dropped to levels similar to those in the morning, but the chick then started to regularly alternate brooding and foraging bouts and maintained T_b around 39°C with a minimum of 37.5°C. In the following days, T_b was maintained around 38-40°C, with a minimum of 37.9°C measured at 4 days of age, even though T_a reached values as low as 4°C during this period (fig. 8.1 lower panels). Until four days of age, T_b decreased during foraging bouts under colder ambient conditions, and increased during brooding bouts. T_b of the second chick was measured at 3 days of age only. It maintained a stable T_b

around 40°C throughout the afternoon, also when T_a dropped below 15°C. When T_a decreased further in the evening hours, T_b decreased during foraging bouts, to a minimum of 36.5°C, and increased again to values around 40°C during brooding.

In general, foraging bouts lasted longer with increasing ambient temperature and age (fig. 8.2). The effect of ambient temperature on foraging bout length was stronger than the effect of age (general linear model in SPSS 17 on the logarithm of foraging bout length; effect of T_a: $F_{1,\,418} = 132$, $P < 0.0001$; effect of age: $F_{1,\,418} = 14$, $P < 0.01$; $r^2_{\text{model}}=0.25$ (no interaction $T_a \times$ age). At eight days old, whimbrel chicks still spent time being brooded, although T_b remained stable during foraging bouts at colder periods, indicating that the birds were homeothermic under those ambient temperatures.

Rectal temperature of foraging chicks

Body temperature of whimbrel chicks, foraging and brooding in an enclosure, was 39.9°C on average (min 36.5 after learning to use brooder to rewarm – max 42.4°C, core temperatures as measured with internal transmitter). On average T_b did not show a clear change with increasing age (1 through 16 d), but variation in T_b was much higher in younger chicks (fig. 8.3). Rectal temperatures of whimbrel chicks, once they had learned to find the brooder, was 36.8ºC at minimum, and thus highly similar to core body temperatures measured with the transmitter. Chicks that were still learning to use the brooder had lower rectal temperatures, with a minimum of 28.9ºC.

Similar results were found for chicks of least sandpiper, dunlin, lesser yellowlegs and godwits (fig. 8.4). Rectal temperatures of these species were 39.5ºC on average and this average did not change with age. However, similar to the whimbrel chicks, T_b showed large fluctuations at early ages, between 32.9 and 44.8ºC. Chicks that were still learning to use the brooder had lower temperatures, similar to whimbrel chicks.

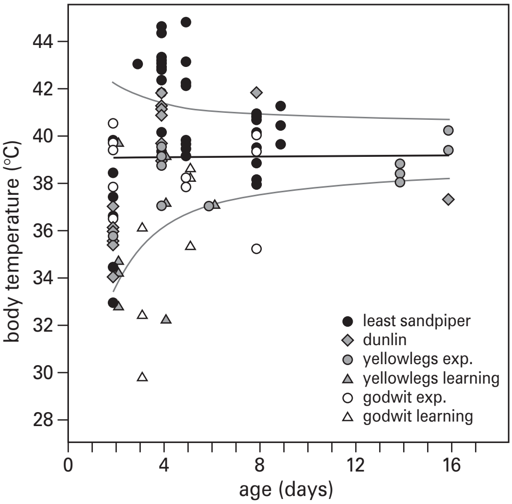

Figure 8.4. Body temperatures of chicks of least sandpiper, dunlin, lesser yellowlegs and Hudsonian godwit in relation to age. Temperatures measured rectally. Body temperatures of chicks that were still learning to find the brooder (triangles) dropped considerably more than those of experienced chicks (circles). Lines depict the regressions of minimum, maximum (grey lines, fitted with inverse function) and mean (solid line; linear function) temperatures.

Effect of ambient temperature

During the measurements, ambient temperatures ranged between 1 and 32ºC, with an average of 14ºC. On average, dunlin chicks were measured under the coolest conditions, while least sandpipers were measured under the warmest conditions. For a given species at a given age, ambient temperatures varied 10ºC between measurements on average, with the largest range between minimum and maximum temperature in whimbrel (14ºC) and the smallest range in least sandpiper chicks (6ºC).

Body temperatures of chicks were higher when ambient temperatures were higher. This was true for all species investigated (fig. 8.5) (general linear model in SPSS 17: species as fixed factor; effect of ambient temperature: $F_{1,\,1545} = 347$; $P < 0.001$; $r^2 = 0.33$). T_b was not correlated to wind and radiation. Body

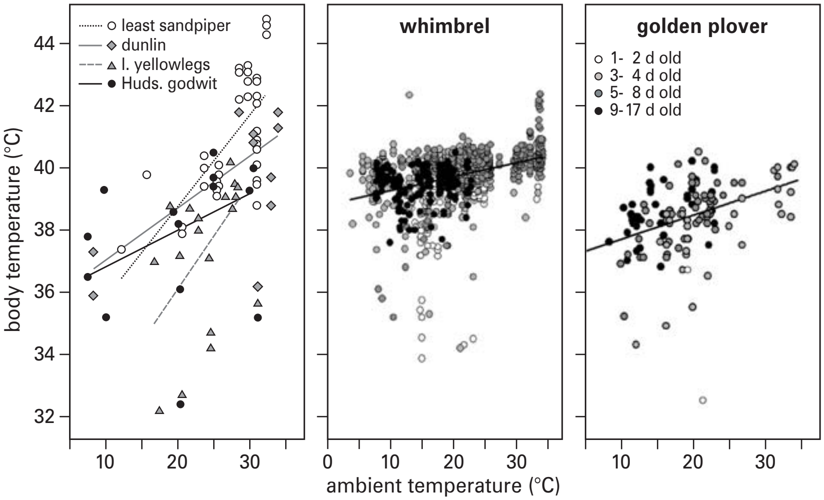

Figure 8.5. Body temperature in relation to ambient temperature for various sized chicks of six species of shorebirds, during either cooling or warming behaviour.

temperature did not increase significantly with age of the chicks.

The exceptionally high rectal temperatures that were measured in the least sandpiper chicks (fig. 8.4) was partly due to the high ambient temperatures at the time of the measurements ($T_a > 30$°C). However, also under comparable ambient temperatures, T_b still showed considerable variation.

Discussion

Body temperature maintained at 35°C or more

Foraging chicks of precocial shorebirds did not voluntarily lower their body temperature below 35°C. Under thermoneutral conditions, T_b of precocial chicks lies around 40°C, but they are able to survive body temperatures as low as 26°C (Myhre & Steen 1979), and can remain mobile at T_bs of around 32°C (Brown & Downs 2002, Krijgsveld *et al.* 2003b). Despite this high level of flexibility, body temperatures were kept at relatively high levels during foraging.

Our finding that chicks do not normally lower their body temperature below 35°C is in agreement with earlier studies on precocial species that investigated body temperatures of non-homeothermic chicks under voluntary foraging behaviour (Myhre & Steen 1979, Pedersen & Steen 1979, Brown & Downs 2002). These chicks returned to be rewarmed before body temperatures fell below 34-38°C. Also observations on free-living chicks of American golden plovers and on chicks of Japanese quail experimentally exposed to low ambient temperatures, similarly showed that body temperatures were maintained at levels of 35°C or more (Krijgsveld *et al.* 2003a,b). Unfortunately, few studies have reported body temperatures during voluntary foraging behaviour. Only when chicks were forcibly exposed to low ambient temperatures, did body temperatures drop to lower levels (Myhre & Steen 1979, Eppley 1984, Gdowska *et al.* 1993). We found two studies in which body temperatures during voluntary foraging were below the values we found. One concerns the observation of two chicks of redshanks (*Tringa totanus*) that were foraging voluntarily at rectal temperatures of 26°C (Myhre & Steen 1979). The other study concerns foraging chicks of avocets (*Recurviro-*

stra avosetta), where 7 out of 65 rectal measurements showed body temperatures between 28 and 32°C for very young chicks (< 50 g), although average body temperature for these chicks was 36°C (Joest 2003). We cannot explain why these chicks would have exhibited such low body temperatures. It takes a while to approach and then locate chicks that are foraging under natural conditions. From laboratory measurements it is known that once chicks start cooling, their body temperatures drop increasingly fast, up to a degree per minute under cold conditions (see Krijgsveld *et al.* 2003a, Ricklefs & Williams 2003). Possibly body temperatures had decreased by the time the chicks were located and temperatures were measured. Chicks, especially very young ones, hunker down on the ground in case of alarm, which may increase the loss of body heat. This effect will be larger when the ground is wet, such as often is the case in foraging habitat of avocet families. Indeed, the avocet chicks with the lowest body temperatures were crouching on bare ground or in short vegetation at capture, which may have resulted in slightly lower body temperatures than normal (pers.comm. R. Joest).

Low body temperature can have several negative consequences for shorebird chicks, including reduced growth rate (Krijgsveld *et al.* 2001 [chapter 4], Gillooly *et al.* 2002, Kristan & Hammond 2002), reduced locomotor ability (likely affecting prey capture rate; Norton 1973, Aulie 1976, Bennett 1990, Choi & Bakken 1991, Rojas 2012, own observations), and reduced rate and efficiency of digestion (Kleiber & Dougherty 1934, Osbaldiston 1966, see also chapter 7). In addition, energy expenditure during foraging is high (Schekkerman & Visser 2001, Krijgsveld *et al.* 2012 [chapter 5]), and the metabolic rate of a chick initially increases in order to maintain high body temperatures (Ricklefs & Williams 2003). Furthermore, lowering body temperature does not result in increased overall foraging time (see below).

Body temperature with respect to environmental conditions

Environmental conditions during the measurements were generally not very stressful owing to moderate ambient temperatures and reasonably good food availability. Chicks have been shown to lower their body temperature more when weather conditions are colder (Krijgsveld *et al.* 2003a,b; chapters 6&7). Under conditions where foraging time is more constrained, for instance because of poor food availability or low ambient temperatures, minimum body temperatures may be lower than was measured in this study. Such low temperatures may be related to the balance between foraging time and brooding time. Under lower ambient temperatures, chicks will cool faster under the same activity pattern and at the same level of energy production. Possibly, the balance shifts towards lower body temperature at the end of a foraging bout when conditions are colder. However, this relationship should be investigated in more detail.

Lower minimum body temperature results in reduced foraging time

By modeling the rate of heat loss, and varying the minimum T_b at which chicks continue to forage, we can calculate the length of foraging and brooding bouts, and thus the percentage of time available for foraging. For an explanation of the model used, see Krijgsveld *et al.* 2003b. Briefly, the cooling rates of chicks were calculated by subtracting the amount of heat lost through wet thermal conductance from the metabolic heat production of the chick (following eq. 5 in Visser & Ricklefs 1993a). Brooding bouts increased in length as minimum T_b was lower, and this increase is steeper than the increase in foraging bout length. Therefore the overall percentage of time that can be spent on foraging was lower when minimum T_b was lower (fig. 8.6 upper panels). In this figure, data are shown for chicks of the least sandpiper. Modeled data from chicks of the other species (dunlin, lesser yellowlegs, Hudsonian godwit, American golden plover) show similar results.

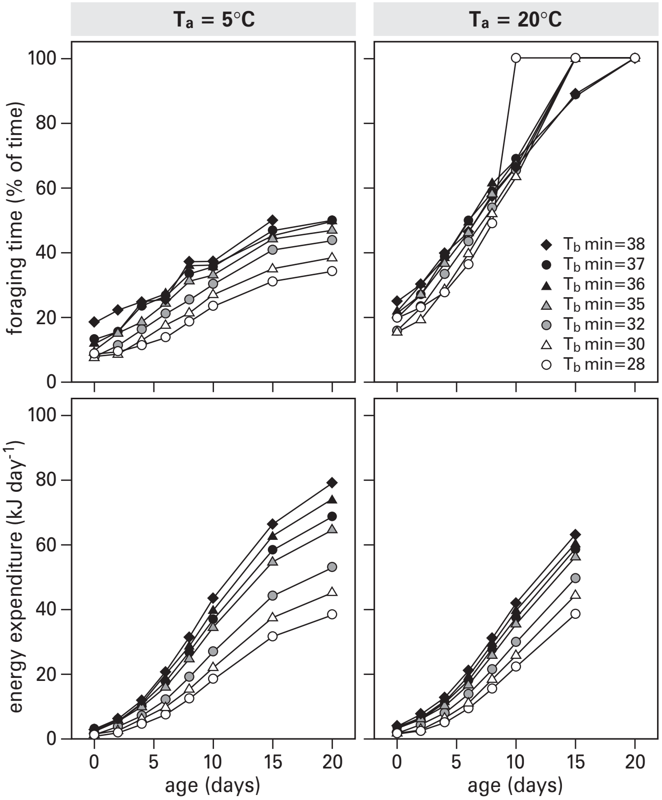

Figure 8.6. Modeled foraging time (top) and energy expenditure (bottom) of chicks of least sandpiper under varying minimum values of T_b, shown for a low (left) and a high (right) ambient temperature. Foraging time decreases rather than increases when minimum T_b is lower, although energy expenditure goes down as well.

Thus, the overall amount of time spent foraging will not be longer when body temperature is dropped further, and possibly even decreases in proportion to the increase in brooding time that is needed to regain body heat. This result can be understood if we consider the fact that body temperature drops increasingly fast when the chick continues foraging (Krijgsveld *et al.* 2003a,b; chapters 6 & 7), and therefore little foraging time is gained with each degree of body temperature lost. In addition, the subsequent passive rewarming means that the time needed for the chick to rewarm increases as initial body temperature decreases (fig. 8.7).

Limitations of the model

Our model assumes a rate of heat loss measured in a small metabolic chamber that restricted movement, and so loss of body temperature may be unrealistically rapid. Under natural conditions, foraging activity considerably elevates heat production compared to that measured in metabolism chambers (Bruinzeel & Piersma 1998, Ellerby *et al.* 2003). As a result, cooling will be slower thus lengthening the foraging bout, while the chick continues to function at peak levels of energy expenditure. Thus, foraging bouts may in reality be longer than in our model, because chicks can continue foraging longer while maintaining their body

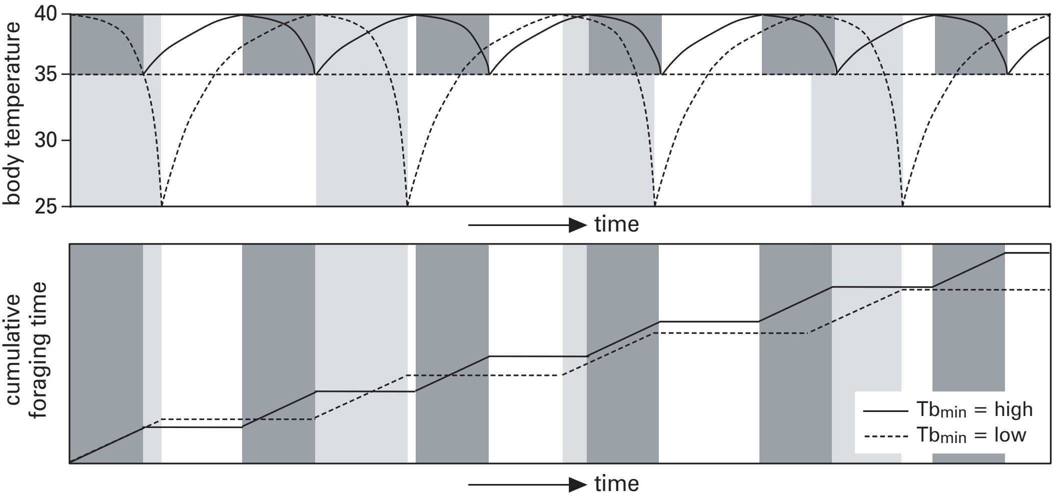

Figure 8.7. Hypothetical diagram of the duration of foraging and brooding bouts when chicks maintain different minimum body temperatures, illustrating that overall foraging time increases when chicks maintain Tb at higher levels. Upper panel: T_b as function of time, of chicks foraging until T_b = 35°C or 25°C at mimimum (continuous resp. dashed line). Foraging bouts shown in grey (light grey: minimum T_b 25°C; dark grey: 35°C). T_b decreases increasingly fast during foraging, and increases during passive rewarming while being brooded by the parent. Lower panel: cumulative foraging time under both conditions.

temperatures. Although this would lead to an overall increase in the percentage of time that can be spent foraging, the percentage of time spent brooding would still increase disproportionally if body temperature were lowered further, as indicated by modeling the effects of a reduced cooling rate.

Lower minimum body temperature is advantageous to the energy budget

Overall energy expenditure, as calculated in the model, was lower when minimum body temperature was lower (fig. 8.6 lower panels). Because foraging chicks operate at levels close to peak metabolic rate (Krijgsveld *et al.* 2012; chapter 5) and because metabolism decreases once T_b has started to decrease substantially (Ricklefs & Williams 2003), levels of energy expenditure will be lower when chicks continue to forage while their T_b is decreasing. Additionally, rewarming is a passive process and thus does not involve a substantial energy metabolism (Ricklefs & Williams 2003). The long rewarming bouts that result from lowering minimum T_b therefore results in a reduced overall EE compared to when minimum T_b is maintained at higher levels. However, the point when T_b starts to decrease substantially and metabolism starts to decrease, may well be the time that locomotory performance of the chick starts to decrease as well. This would render further continuation of foraging unfavourable, despite energetic benefits. Whether such a loss of functional capacity coincides with lowered body temperatures and decreased metabolism would need to be investigated.

In conclusion

Foraging chicks of precocial shorebirds did not voluntarily lower their body temperature below 35°C, even though they are able to remain mobile at lower body temperatures. Cooling below 35°C was shown by modeling to have negative effects on the percentage of time that could be spent foraging in comparison to the time needed for rewarming under the parent. Low body temperatures thus are not profitable for growing and self-foraging precocial chicks. They can survive body temperatures well below 30°C, and this greatly benefits survival chances when chicks involuntarily have to endure extended periods of cooling, but voluntary hypothermia does not benefit growth. Instead, by minimizing foraging bout length and increasing brooding time, and thus maintaining a high body temperature, chicks can considerably reduce energy expenditure, while simultaneously increasing rate and efficiency of digestion.

Acknowledgements

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Chapter 9

Summary

Karen L Krijgsveld

Research question

This thesis is about the development of precocial shorebird chicks in relation to demands set by their arctic environment. Newly hatched shorebird chicks must grow rapidly to achieve independence before the end of the short arctic growing season. A rapid growth rate may, however, conflict with development of the functional capacity required to walk and generate heat. We investigated how chicks of both smaller and larger species of shorebird physiologically resolve the postulated conflict between rapid growth rate and the development of functional capacity. In addition, we investigated how chicks deal behaviourally with the boundaries set by their physiology and the environment, in order to maximize growth.

To address these issues, we studied growth rate and functional capacity as well as foraging and thermoregulatory behaviour of seven species spanning the full range of body size among shorebirds, and related chick foraging behaviour to food abundance. Subjects of the study were, with one exception (Japanese quail), chicks of shorebirds breeding on the subarctic tundra at Churchill, Canada.

Physiological adaptations: growth rate and functional maturity

To investigate how growth rate relates to functional maturity levels of precocial chicks, we related chick growth rate to levels of functional capacity. Growth rate calculated as proportion of asymptotic size was highest in chicks of the smallest species (chapter 2), in line with comparisons across a broader taxonomic range. The larger species (Hudsonian godwit and whimbrel) required more time to complete growth than the smaller species. However, growth rate of these two species was high for their size, in comparison to other similarly sized shorebird species.

Functional capacity, measured by means of the activities of enzymes involved in the major catabolic pathways (chapter 4), and the daily energy expenditure of chicks living under semi-natural conditions (chapter 5), revealed that chicks of smaller species, which grow faster, also exhibit greater functional capacity than chicks of larger species. In addition, the high levels of daily energy expenditure compared to levels of cold-induced peak metabolic rates in immobile chicks measured in another study, suggest that locomotion produces substantial quantities of heat, supplementing or even replacing the need to shiver.

In conclusion, chicks of small arctic sandpipers, which are among the smallest homeotherms, are remarkable for maintaining high levels of metabolic activity while simultaneously growing rapidly. The chicks of larger species also grow rapidly to achieve adult size during the brief arctic growing season, but their lower thermal conductance and heat loss results in lower mass-specific daily energy expenditure when compared to smaller species. The combination of rapid growth and high functional capacity in small species compared to larger species, contradicts the growth rate – mature function trade-off. However, the results suggest that in conditions where ambient temperature limits the development of chicks, maturation of function is favoured at the cost of growth. Chicks of precocial species thus seem to have considerable latitude to modify this relationship, and larger and smaller species adopt different strategies of growth and tissue maturation (fig. 9.1).

Behavioural adaptations: foraging behaviour and body temperatures

Next we investigated how the physiological capacities of precocial chicks determine the time available for foraging, and how the chicks adapt behaviourally to the variable and often adverse weather conditions. One of the key variables is body temperature of the chicks, because it affects the amount of time they have for foraging, and it therefore is an important aspect in survival. Young precocial chicks are not homeothermic and have highly variable body temperatures. Typically, body temperature decreases during foraging. The chicks can survive body temperatures well below 30ºC, and this benefits their survival chances when they involuntarily endure extended periods of cooling. However, lowering body temperature has significant disadvantages, such as reduced muscle performance and locomotor ability, likely affecting prey capture rate.

In a series of studies on shorebird chicks under natural or semi-natural conditions, and on Japanese quail chicks exposed experimentally to either high or low ambient temperatures (24 or 7ºC), we found that precocial chicks do not lower their body temperature below ca. 36ºC when foraging, and instead return to the parent to be rewarmed (chapters 6-8). Below this temperature, the disadvantages related to physiological processes, such as increased energy expenditure and reduced rate and efficiency of food intake (chapter 7), apparently outweigh the advantages of continued foraging. Because body temperature drops at an accelerating rate when the chick continues foraging (chapters

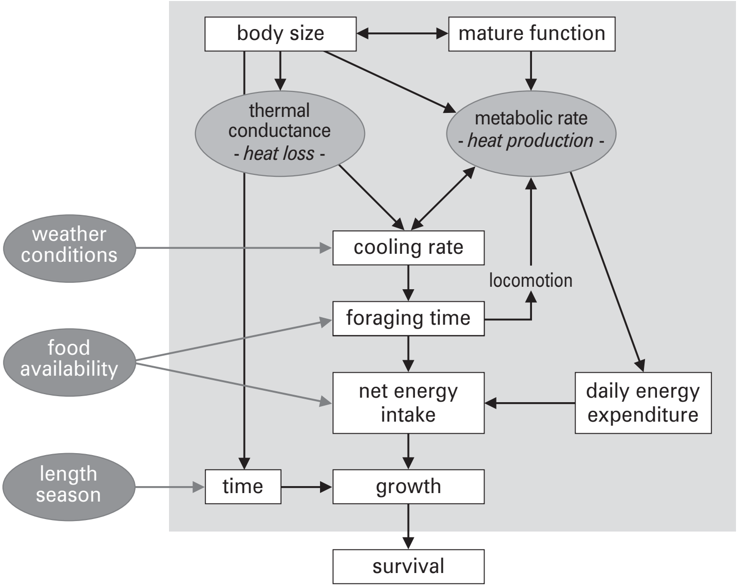


Figure 9.1. Schematic diagram showing the main aspects affecting growth and ultimately survival that were studied in this thesis. Chicks of larger species rely on their body size to limit heat loss, resulting in lower mass-specific metabolism, but simultaneously they need more time to complete growth. Chicks of smaller species rely more on functional capacity of muscle tissue to generate heat and prevent cooling, at the cost of high mass-specific energy expenditure, while at the same time they grow fast. Environmental conditions such as weather, food availability and length of the season present external constraints limiting growth, and the chicks respond to this by adjusting their behaviour and physiology.

6 & 7), little foraging time is gained with each degree of body temperature lost, while the subsequent passive rewarming disproportionately increases the time needed for the chick to rewarm. Modelling the rate of heat loss in shorebird chicks indeed showed that a further reduction of body temperature did not increase the available foraging time, but rather reduced it, due to a disproportionate increase in brooding time needed to regain body heat (chapter 6). These findings contrast with the pervasive notion that precocial chicks use their ability to remain active at lower body temperatures to prolong foraging bouts.

In conclusion, by ending foraging bouts at body temperatures of ca. 36°C, chicks avoid the increase in energy expenditure and decrease in motor function that are related to a further decrease in body temperature. As a result, the chicks have more time available for foraging compared to extending foraging bouts at the cost of body temperature, and they thus maximize growth (fig. 9.1).

In conclusion

I have shown that precocial chicks of shorebirds have evolved to combine a high growth rate with high levels of functional capacity, and that they feature substantial flexibility in development and foraging behaviour to adjust to demands set by varying ambient conditions.

The main findings are:

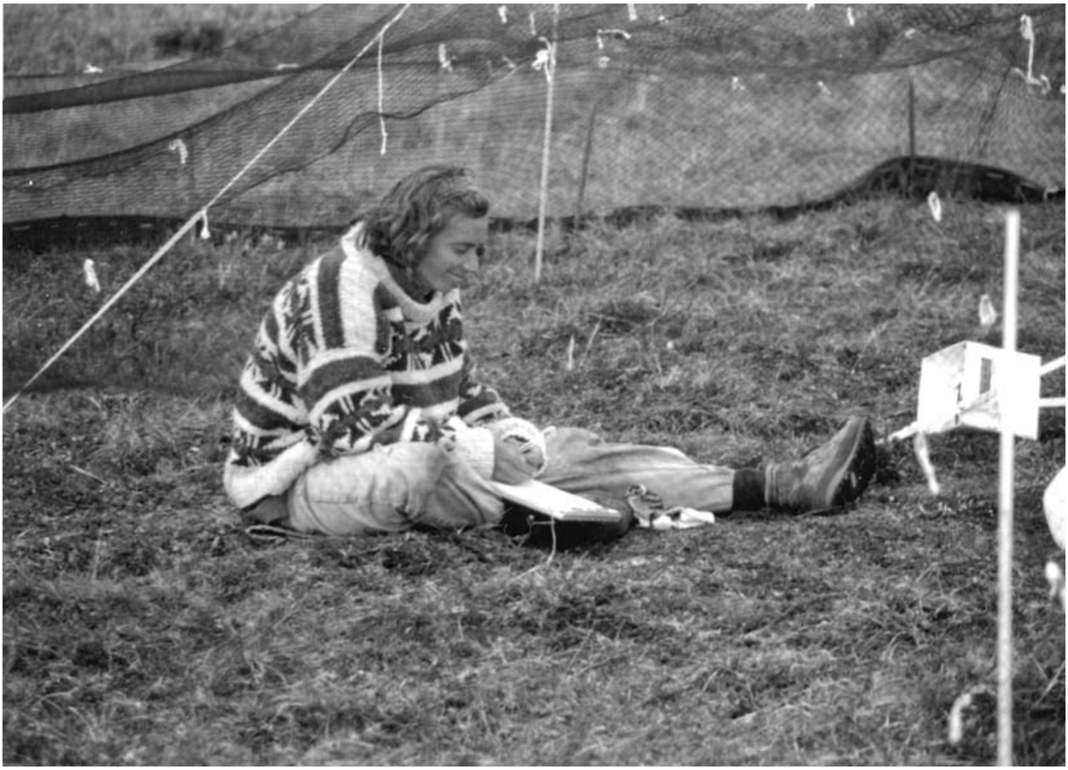
1. Chicks of small species combine a high level of mature function (*i.e.* catabolic capacity and daily energy expenditure) with high growth rates, while larger species limit functional capacity in favour of growth.

2. Low ambient temperatures can result in a shift in the balance between growth rate and mature function, in favour of mature function.

3. Mature function is not necessarily challenged by low ambient temperatures, because chicks reduce foraging bout lengths in response to low ambient temperatures in order to limit heat loss and daily energy expenditure.

4. Growth is maximized by maintaining minimum body temperature at relatively high levels of 36-37°C.

The research presented in this thesis shows that shorebirds provides a good model for understanding physiological and behavioural adaptations of homeothermic organisms to cold environments with limited periods available for reproduction and development, as well as for investigating trade-offs between functions under stressful conditions.



Chapter 10

Nederlandse samenvatting

Achtergrond: Groeien of warm blijven?

Dit proefschrift gaat over de groei van steltloperkuikens. De **groei** van een dier omvat talloze fysiologische en gedragsmatige veranderingen. De meest opvallende verandering, en datgene wat we doorgaans verstaan onder 'groei', namelijk toename in grootte, is hier slechts één van. Groei is echter onlosmakelijk verbonden met ontwikkeling, waarbij de functionele capaciteit van het weefsel veel belangrijker wordt dan de toename in grootte. Die functionele capaciteit wordt bereikt doordat weefselcellen zich differentiëren. Hierbij valt bijvoorbeeld te denken aan de ontwikkeling van spieren en daarmee van motorfunctie, die een dier beter in staat stellen om te foerageren en voedsel te verteren. En ook de onwikkeling van **gedrag** gaat hieraan gepaard, zoals bedelen om of zoeken naar voedsel, warmte zoeken bij een ouder, of de interactie met nestgenoten.

Steltloperkuikens zijn bij uitstek afhankelijk van omgevingsomstandigheden. Zij zoeken vanaf dag één zelf buiten het nest hun voedsel bij elkaar (het zijn nestvlieders), maar kunnen aanvankelijk hun lichaamstemperatuur niet op peil houden en moeten daarom regelmatig bebroed worden door een ouder om weer op te warmen. Zeker in de Arctische gebieden, waar steltlopers in hoge dichtheden broeden, heeft de omgeving veel invloed op de groei van de kuikens. Het broedseizoen duurt maar kort, wat vraagt om een snelle groei. Tegelijkertijd kunnen de temperaturen er erg laag zijn, wat vraagt om een goeie thermoregulatie. Hoe gaat een kuiken hiermee om?

Het vermogen van een kuiken om zijn **lichaamstemperatuur** op peil te houden, is afhankelijk van de functionele capaciteit van de skeletspieren. Die spieren zijn namelijk de belangrijkste bron van warmteproductie in reactie op kou, zowel in jonge als in volwassen vogels. Een grote functionele capaciteit is dus belangrijk voor kuikens op de toendra, maar brengt tegelijkertijd ook beperkingen met zich mee. De capaciteit om warmte (*i.e.* energie) te genereren is namelijk afhankelijk van cellulaire processen, zoals samentrekkende eiwitten en stofwisselingsprocessen. Het lijkt erop, blijkens een aantal studies, dat de ontwikkeling van zulke processen niet samen kan gaan met groei, omdat op celniveau het vermogen om te delen (*i.e.* groei) vaak verloren gaat wanneer cellijnen zich differentiëren. Dit impliceert dat de groeisnelheid van spierweefsel omgekeerd gecorreleerd is aan de functionele capaciteit van dat weefsel. Er lijkt dus een **trade-off** te bestaan tussen de twee: spieren die snel groeien kunnen niet ook tegelijkertijd veel energie of warmte produceren. Dit heeft consequenties voor de groeipatronen van steltloperkuikens in de Arctische gebieden, waar zowel warmteproductie als snelle groei belangrijk zijn.

Onderzoeksvragen

Het onderzoek beschreven in dit proefschrift gaat in op de vraag hoe steltloperkuikens van grotere en kleinere soorten de balans vinden tussen groei aan de ene kant en functionele capaciteit aan de andere kant. Daarnaast onderzoeken we hoe kuikens hun gedrag en fysiologie aanpassen aan de vaak veeleisende weersomstandigheden op de toendra, teneinde maximaal te kunnen groeien.

Aanpak

Het onderzoek is uitgevoerd aan de kuikens van zeven soorten steltlopers en van de Japanse kwartel. Het practische werk aan de steltloperkuikens is gedaan op de Canadese toendra bij Churchill in de provincie Manitoba. Dit gebied herbergt hoge dichtheden van veel verschillende soorten steltlopers. Er is daarbij veel diversiteit in soortsgrootte, wat vereist was om verschillen in groeistrategieën te kunnen onderzoeken. De onderzochte soorten liepen op in lichaamsgrootte: de kleinste soort, de kleinste strandloper, woog 4 gram bij uitkomst uit het ei; de grootste soort, de wulp, 20 gram. Het gebied ligt aan de kust van de Hudson Bay, waar koude noordelijke winden en warmere zuidelijke winden kunnen zorgen voor grote schommelingen in de omgevingstemperatuur. Dit stelde ons in staat de effecten van weersomstandigheden op foerageergedrag en fysiologie te onderzoeken.

Deel 1: Groeisnelheid en voedselaanbod

Allereerst zijn twee basale aspecten in kaart gebracht: groeisnelheid van de kuikens en het voedselaanbod op de toendra. Met deze gegevens kunnen we de resultaten over fysiologie en gedrag, die in deel 2 en 3 worden gepresenteerd, beter interpreteren.

In **hoofdstuk 2** vergelijken we **groeipatronen** van kleinere en grotere soorten steltlopers. Kleinere soorten groeiden sneller dan grotere soorten. De kleinere soorten (bontbekstrandloper en kleinste strandloper) groeiden het snelst, terwijl de grotere soorten (regenwulp en rode grutto) de meeste tijd nodig hadden om hun groeiperiode af te ronden. De kleinste soorten waren bij uitkomst uit het ei procentueel ook het verst in groei (ten opzichte van het volwassen gewicht). Dat kleinere soorten relatief sneller groeien laat zien dat in principe een trade-off tussen groeisnelheid en functionele capaciteit ook van toepassing kan zijn binnen de groep van steltlopers. De grotere soorten, die relatief weinig warmte aan hun omgeving verliezen (door hun gunstiger oppervlakte-volume-verhouding), investeren mogelijk relatief weinig in functionele capaciteit en meer in groei, wat hun totale groeiperiode zou kunnen verkorten (zie hoofdstuk 4&5). Dit is gezien het korte Arctische seizoen vooral voor grotere soorten van belang.

Hoofdstuk 3 gaat in op de variatie in het **voedselaanbod** voor de kuikens. De kuikens eten voornamelijk insecten. Gedurende het broedseizoen hebben we met behulp van plakstrips en potvallen het aantal insecten en spinnen gemeten. Het aantal gevangen insecten varieerde sterk, en was bijvoorbeeld lager wanneer het koud was of hard waaide. Het voedselaanbod liep synchroon met de voedselbehoefte van de kuikens, in die zin dat het overeenkwam met de periode dat de kuikens uitkwamen, en het meeste voedsel nodig hadden. Ook was het aanbod aan kleinere insecten het grootst in de periode dat er kleine kuikens waren, die dit type voedsel bij voorkeur eten, terwijl de grotere insecten beschikbaar waren op het moment dat de kuikens groter waren en dus grotere prooien selecteerden, en ook een grotere voedselbehoefte hadden. Door de dag heen was het insectenaanbod overdag aanzienlijk groter dan 's nachts. Het aantal gevangen insecten was het hoogst laat op de ochtend, wat gereflecteerd werd in het foerageergedrag van goudplevierkuikens (zie hoofdstuk 6).

Deel 2: Groei versus functie

In dit deel gaan we in op de relatie tussen groeisnelheid en functionele capaciteit, ofwel tussen groeien of warm blijven. Nestvliedende kuikens in het Arctische gebied moeten snel groeien om aan het eind van het korte broedseizoen vliegvlug te kunnen zijn. Die snelle groei zou echter kunnen conflicteren met de ontwikkeling van functionele capaciteit die nodig is om te lopen (foerageren) en om warmte te genereren. Die functionele capaciteit hebben we op twee manieren gemeten: door te bepalen hoeveel energie de spieren kunnen genereren, en door de dagelijkse energie-uitgave van de kuikens te meten.

In **hoofdstuk 4** onderzoeken we of de **catabole capaciteit**, ofwel het vermogen van de spieren van de kuikens om energie te genereren, lager is in sneller groeiende spieren dan in langzamer groeiende spieren. We hebben de catabole capaciteit gemeten in de poot- en vliegspieren van de kleinere bonte strandloper en de grotere regenwulp, en vergeleken met de groeisnelheid van die spieren. Binnen de twee onderzochte soorten steltlopers was de catabole capaciteit hoger in de pootspieren dan in de vliegspieren, vooral in jonge kuikens, wat past bij het feit dat de kuikens allereerst moeten kunnen lopen, terwijl vliegen pas later van belang is. De bonte strandlopers groeiden niet alleen snel, maar hadden in het algemeen ook een grotere catabole capaciteit, vooral in de vliegspieren. Dit wijst erop dat kuikens van de kleine bonte strandloper afhankelijker zijn van catabole capaciteit voor de productie van warmte, terwijl de grotere wulpenkuikens dankzij hun grotere volume meer warmte vasthouden en daardoor toe kunnen met een kleinere functionele capaciteit. Dit resultaat is in strijd met een trade-off tussen groei en functionele capaciteit, en wijst erop dat nestvliedende kuikens de verhouding tussen de twee kunnen aanpassen. Grotere en kleinere soorten lijken daarbij verschillende strategieën te volgen.

In **hoofdstuk 5** onderzoeken we de **dagelijkse energie-uitgave** (DEE) van de kuikens en de relatie met lichaamsgrootte. Dit hebben we gemeten met behulp van de zwaar-water-methode aan kuikens van vijf soorten steltlopers van verschillende grootte. De kuikens zaten buiten in een omheining waar ze foerageerden en blootgesteld waren aan het weer. Kleinere soorten hadden per gram gewicht een hogere dagelijkse energie-uitgave dan grotere soorten, in overeenstemming met hun hogere catabole capaciteit. De dagelijkse energie-uitgave was vergelijkbaar met de maximale stofwisselingssnelheid die is gemeten door blootstelling aan lage temperaturen in metabolismekamers, waarbij de kuikens niet konden bewegen. Dit wijst erop dat beweging (foerageren!) een vergelijkbare hoeveelheid warmte oplevert als bibberen. De omgevingstemperatuur had geen significant effect op de dagelijkse energie-uitgave. Mogelijk komt dit doordat de kuikens tijdens het lopen genoeg warmte produceerden om warm te blijven, ook al omdat het in de onderzoeksjaren doorgaans niet bijzonder koud was in Churchill (gemiddeld 12°C in juli). Bovendien zaten de kuikens meer onder de ouder wanneer het kouder was (hoofstuk 6), waardoor hun energie-uitgave ook lager was (hoofdstuk 7). Ook dit resultaat spreekt het bestaan van een trade-off tussen groeisnelheid en functionele capaciteit tegen, en suggereert veeleer dat nestvliedende kuikens de verhouding tussen de twee aanzienlijk kunnen aanpassen aan de omgevingsomstandigheden.

Deel 3: Aanpassingen in gedrag en fysiologie

In dit deel hebben we onderzocht hoe de kuikens zich qua gedrag en fysiologie aanpassen aan de wisselende en vaak ongunstige weersomstandigheden op de toendra. Lichaamstemperatuur speelt hierin een sleutelrol, omdat het het foerageergedrag in belangrijke mate bepaalt.

In **hoofdstuk 6** onderzoeken we hoeveel tijd nestvliedende kuikens hebben om te foerageren, en hoe dit bepaald wordt door hun fysiologische capaciteiten. Daartoe hebben we het **foerageer- en opwarmgedrag** van kuiken van vrijlevende families goudplevieren onderzocht, en ook van goudplevierkuikens onder semi-natuurlijke omstandigheden buiten in een omheining. Steltloperkuikens wisselen foerageerrondes altijd af met periodes onder de oudervogel om weer op te warmen.

Naarmate het warmer was, en ook naarmate de kuikens ouder werden, duurden de foerageerrondes langer en hadden ze in totaal meer foerageertijd. Laat in de ochtend wanneer het voedselaanbod hoog was (hoofdstuk 3) duurden foerageerrondes langer dan op andere momenten van de dag. De grote variatie in de duur van foerageerrondes wijst erop dat in Churchill de relatief milde temperaturen niet beperkend waren voor de foerageertijd en de ontwikkeling van de kuikens, en dat ook andere factoren van invloed waren, zoals voedselaanbod. De **lichaamstemperatuur** van de kuikens was lager wanneer het kouder was, en varieerde sterk in jonge vogels, maar was nooit lager dan 36°C aan het eind van een foerageerronde. Dit resultaat is in tegenspraak met de algemene opvatting dat nestvliedende kuikens zich ver af laten koelen om zo langer te kunnen foerageren.

In **hoofdstuk 7** onderzoeken we het effect van **koude omstandigheden** op het foerageergedrag en de fysiologie van nestvliedende kuikens. Hiertoe hebben we één groep kuikens van Japanse kwartels experimenteel blootgesteld aan een hoge omgevingstemperatuur (24°C) en de andere groep aan een lage omgevingstemperatuur (7°C). Het foerageergedrag in relatie tot omgevingstemperatuur en leeftijd leek erg op dat van de goudplevieren (hoofdstuk 6). En net als de goudplevieren beëindigden de kuikens hun foerageerrondes bij een lichaamstemperatuur van minimaal 37°C. Kuikens die waren blootgesteld aan lage omgevingstemperaturen hadden een hogere totale voedselopname om te compenseren voor de eveneens hogere energie-uitgave. De groeisnelheid was in eerste instantie lager, maar nam na ca. één week toe, waardoor de aan kou blootgestelde kuikens op een leeftijd van drie week groter waren dan de kuikens die in de warmte waren opgegroeid. Deze resultaten wijzen erop dat wanneer de omgevingstemperaturen zo laag zijn dat ze beperkend worden voor de ontwikkeling van het kuiken, dat dan meer geïnvesteerd wordt in de ontwikkeling van functie, ten koste van de groeisnelheid.

In **hoofdstuk 8** onderzoeken we hoe het nou precies zit met de **lichaamstemperaturen** van foeragerende kuikens. Zowel vrijlevende goudplevierkuikens in Churchill, als kwartelkuikens die experimenteel werden blootgesteld aan lage temperaturen, lieten tijdens het foerageren hun lichaamstemperatuur niet onder de 36°C zakken, terwijl ze ook veel lagere lichaamstemperaturen toch goed kunnen overleven (hoofdstuk 6&7). We hebben daarom de lichaamstemperaturen van diverse soorten steltloperkuikens gemeten, foeragerend onder semi-natuurlijke omstandigheden in omheiningen op de toendra. De lichaamstemperatuur werd rectaal gemeten, en bij wulpenkuikens ook met behulp van temperatuurgevoelige radiozendertjes in de lichaamsholte. Kuikens van regenwulp, rode grutto, kleine geelpootruiter, bonte strandloper en kleinste strandloper beëindigden allen hun foerageerronde bij een lichaamstemperatuur boven 35°C. Door het warmteverlies te modelleren werd inzichtelijk dat verder laten zakken van lichaamstemperatuur ook niet zinvol was, omdat het niet leidde tot een toename van beschikbare foerageertijd, maar juist tot een afname. Dit komt doordat de tijd die het kuiken nodig had om weer op te warmen disproportioneel langer werd naarmate het zich verder liet afkoelen. Door hun lichaamstemperatuur op peil te houden middels kortere foerageerrondes kunnen kuikens netto hun voedselopname en groeisnelheid verhogen.

Conclusies

Nestvliedende kuikens zoals die van steltlopers op de toendra groeien op en overleven onder vaak veeleisende omstandigheden. Uit het onderzoek blijkt dat de kuikens zowel fysiologisch als gedragsmatig heel flexibel zijn om zich aan te passen aan deze factoren, en om hun groei en daarmee hun overlevingskansen te maximaliseren.

De fysiologische flexibiliteit blijkt uit de gevonden relaties tussen groeisnelheid en functionele capaciteit. De kuikens van kleine soorten steltlopers verliezen hun warmte relatief snel doordat hun oppervlak relatief groot is ten opzichte van hun volume. Daardoor zijn ze afhankelijker van hun hoge functionele capaciteit om warmte te genereren (hoewel ook beweging in belangrijke mate aan hun warmteproductie bijdraagt). Tegelijkertijd groeien de kleinere soorten sneller, waardoor ze steeds minder snel hun warmte verliezen. De kuikens van de grotere soorten groeien ook snel, om uitgegroeid te zijn voordat het korte Arctische seizoen is afgelopen. Maar door hun grotere volume verliezen deze grotere soorten hun warmte minder snel en ze kunnen daardoor toe met een lagere functionele capaciteit. De snellere groei in combinatie met hogere functionele capaciteit in kleinere soorten ten opzichte van grotere soorten, impliceert dat van een trade-off tussen groei en functionele capaciteit geen sprake is voor steltloperkuikens. In plaats daarvan lijkt de nodige ruimte te bestaan om de relatie tussen groeisnelheid en functionele capaciteit te veranderen, en lijken grotere en kleinere soorten daarbij verschillende strategieën te volgen.

Ook een hoge mate van flexibiliteit in foerageergedrag stelt de kuikens in staat om maximaal te groeien ten koste van zo min mogelijk functieverlies. De tijd die de kuikens besteden aan foerageren is afhankelijk van zowel hun fysiologische beperkingen als van de weer- en voedselomstandigheden. De kuikens blijven evenwel een vrij hoge lichaamstemperatuur houden tijdens het foerageren: wanneer hun lichaamstemperatuur ca. 36°C nadert, stoppen ze met foerageren en gaan onder de ouder zitten om op te warmen. In totaal hebben de kuikens hierdoor meer tijd om te foerageren dan wanneer ze per foerageerronde langer zouden foerageren maar daarbij hun lichaamstemperatuur verder zouden laten zakken. Op deze manier kunnen kuikens netto hun voedselopname en groeisnelheid verhogen.

Box: Een doorsnee dag in Churchill

Churchill Northern Studies Centre, 14 juli, 2 uur 's nachts. Ik sta op na een te korte nachtrust, maak mezelf een ontbijtje klaar voor onderweg, en stap op mijn mountainbike. Ik fiets over de grindweg naar Halfway Point, een stuk toendra direct aan de kust van de Hudson Bay. In de lucht hangt de rode gloed van de zon die net onder de horizon doorschuift. De nacht is kalm en zacht. Ik laat de fiets achter aan de kant van de weg en loop langs een van de vele meertjes de toendra op. Onderweg hoor ik in de verte twee parelduikers naar elkaar roepen. Dan kom ik aan waar ik naartoe wilde: territorium GP5, van een familie goudplevieren met drie kuikens van twee dagen oud. Het vierde kuiken is al verdwenen – opgegeten door een velduil of een blauwe kiekendief misschien. Het observatietentje vanwaaruit we de familie bekijken staat nog op dezelfde plek als gisteren, dus de familie moet nog in het gebied zijn. Binnenin het tentje hoor ik Gabe in beweging komen, zich uitstrekkend na een lange nacht opgevouwen te hebben gezeten op het stoeltje, achter de telesoop en de radio-ontvanger. Hij zegt dat de kuikens gisteravond rond 23:00 uur voor het laatst gefoerageerd hebben, en dat er daarna weinig actie is geweest: de twee temperatuurgevoelige zendertjes die we op de rug van twee van de kuikens hebben geplakt, hebben vanaf die tijd voortdurend een gelijkmatig, hoogfrequent signaal afgegeven. En dat betekent dat de kuikens warmpjes onder een ouder zitten, en niet hebben gefoerageerd. Gabe gaat naar huis, nadat hij me op de hoogte heeft gebracht van het doen en laten van de kuikens afgelopen avond en nacht, en ik installeer me in het tentje met de antenne, radio-ontvanger, timer, telescoop, verrekijker, pen en papier en koffie. En met een flesje DEET en een startpistool, om de zo gevreesde muggen en ijsberen op een afstandje te houden. De lucht wordt nu snel lichter, en al gauw zie ik het eerste kuiken onder de ouder vandaan rennen. De rose-geverfde veertjes op zijn achterwerk maken duidelijk dat het pink-butt is, het oudste kuiken. Even later zie ik ook de andere twee kuikens. Het radiosignaal dat ik ontvang wordt nu ook snel trager, wat bevestigt dat de kuikens in de koude aan het foerageren zijn. Ik verlies de kuikens uit het zicht achter een heuveltje van mos en wilgjes, en het signaal verzwakt. Dan opeens wordt het signaal weer sneller: het kuiken moet weer onder de ouder zitten op te warmen. Maar waar zitten ze? Ik vind het adulte mannetje terug vlakbij de plek waar hij het laatst zat te broeden, net op tijd om pink-butt naar hem toe te zien rennen en zich onder zijn warme veren te wurmen. Eerste foerageerronde; duur 6 minuten, 3:30 's ochtends.

Dit is hoe een normale veldwerkdag in Churchill eruit zag. Ik beschrijf het omdat het een beeld schetst van de leefwereld van een nestvliedend kuiken in de Arctische broedgebieden, en zo de abstracte onderzoeksvragen die in dit proefschrift zijn behandeld concreter maakt.

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One of the major findings of this thesis is that chick body temperature is maintained at high levels. I could not have come to the findings presented in this thesis without the work of my co-workers in the research team at Churchill: Bob Ricklefs, Henk Visser, John Olson, Gabe McNett, Jeroen Reneerkens, Quinten van Katwijk, Jan van Gils who made the first enthusiastic steps in this project, Irene Tieleman, Joe Williams, George Bakken, Dave Pennick, Don Miles, Adrienne Smith and Quiyhn Luong. The cooperation with John Olson was continued at Villanova University in Philadelphia, where we ran enzyme assays almost non-stop to figure out catabolic capacity of chick muscles. I thank him for a very fruitful cooperation, and for making me feel welcome. At home on the Dutch meadows and on the Siberian tundra, Hans Schekkerman did very comparable work on godwit, lapwing and other chicks. It was great to be able to share my thoughts and experiences with him.

I thank the staff of the Churchill Northern Studies Centre; Ray, Marcus, Steacey, Michael, Joan and Barbara for providing us with everything we needed to carry out our research, for making everything run smoothly, for providing us with wholesome food at all hours of the day and night, and for helping us to stay safe from the polar bears.

My current work as an applied ecologist at Bureau Waardenburg allows me to contribute in a small but very satisfactory way to nature protection and conservation. It is even better that I get to do it together with a great team of highly driven bird ecologists. Almost since the first day I started working at Bureau Waardenburg, in May 2002, I have been involved in a very large project: to determine the effects of the OWEZ offshore wind farm at Egmond aan Zee on collision risks and avoidance behaviour of birds. I may have spent more time on this project than on my PhD thesis. In that sense I sometimes think of the OWEZ work as my second PhD project, with a different set of encouraging and motivating colleagues, with excellent field work on the metmast and the NAM gas platform offshore, with challenging analyses, and with a tedious reviewing process. Once the OWEZ work came to a finish, there was space in my head and on my desk to round off my PhD work as well. My colleagues have stimulated me to finish this thesis. Thanks for your friendship, patience and encouragement through the years.

Mijn familie en vrienden zijn mijn niet-aflatende bron van vriendschap, liefde, gezelligheid en steun. Daarmee zijn zij misschien wel het allerbelangrijkst in het bereiken van deze eindstreep. Zonder hun steun had ik het niet volgehouden. Het contact met mijn vrienden was door deze jaren heen wezenlijk voor het uitoefenen van de zo essentiële wetenschappelijke uitwisselingen, vriendschappelijke conversaties en relativerende ontspanning aan het eind van de dag, zij het in een kroeg of thuis aan de eettafel, onder het genoegen van een goed glas bier of wijn.

Het contact met mijn familie, in de vorm van wandelingen, spelletjes, gesprekken en etentjes, in alle mogelijke combinaties, vormt een sterke basis van waaruit ik werk en denk en leef. Zij zullen ook wel blij zijn dat ik dit boekje nu eindelijk af heb, al was het maar omdat het voor hen ook niet mee kan zijn gevallen om 15 jaar lang te onthouden waar dat promotie-onderzoek ook alweer precies over ging, of om rekening te houden met de rol dat in mijn leven speelde. Helemaal omdat ik het er niet over wilde hebben, en er dus tijden lang alleen in codetaal terloops geïnformeerd mocht worden naar dingen die te maken hadden met het P-woord. Maar ik heb veel gehad aan het luisterende oor, het begrip en ook de kritische vragen van mijn broer en zus, en aan de bemoedigende woorden van mijn moeder. En aan de gesprekken en de lol die we samen hebben, met mijn schoonzus en zwager, mijn vijf neven, mijn moeders vriend, en met mijn schoonfamilie. Vorig jaar stond ik met mijn moeder in een natuurgebied ergens in Drenthe te kijken naar een stel jonge kluten dat rondrende op een slikkig oevertje en onder de adult kroop om op te warmen. Het bracht me even terug naar Churchill, juist in een periode dat ik veel in Groningen was om de laatste hoofdstukken van dit proefschrift af te ronden. Hoe toepasselijk! Het feit dat ik daar met haar stond, zoals we samen zoveel andere mooie plekken in Nederland bekeken hebben, maakt wel duidelijk dat ik mijn liefde voor de natuur niet van een vreemde heb.

Mijn vader was degene die altijd inhoudelijke vragen stelde over mijn onderzoek, vertrouwen had in de keuzes die ik maakte, en me aanmoedigde om door te gaan. Misschien heb ik mijn vastberadenheid aan hem te danken. Wat zou hij trots zijn geweest op dit boekje.

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Last but not least my thanks to the magnificent shorebirds of Churchill.

The wind birds (shorebirds) are not credited
with the ability to sing, a disgrace that they
share with all nonmembers of the
Passeriformes – the so-called songbirds.
Yet the calls of shorebirds are often more
melodious than the songs of songbirds.

after Peter Matthiesen in Stout (1967)

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