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Precocial problems

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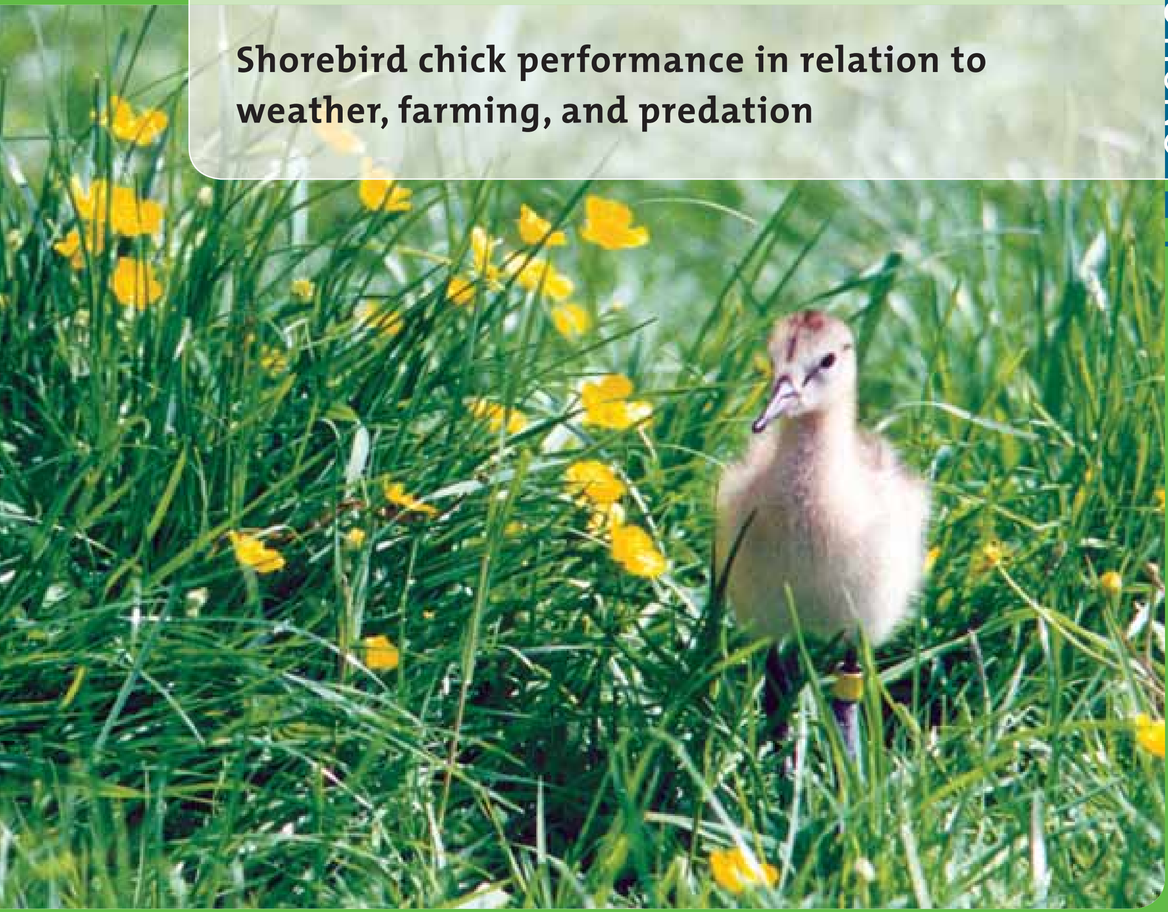
Hans Schekkerman

PRECOCIAL PROBLEMS

Shorebird chick performance in relation to weather, farming, and predation

ALTERRA SCIENTIFIC CONTRIBUTIONS 24



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Shorebird chick performance in relation to weather, farming, and predation

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PRECOCIAL PROBLEMS

Shorebird chick performance in relation to weather, farming, and predation

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Introduction

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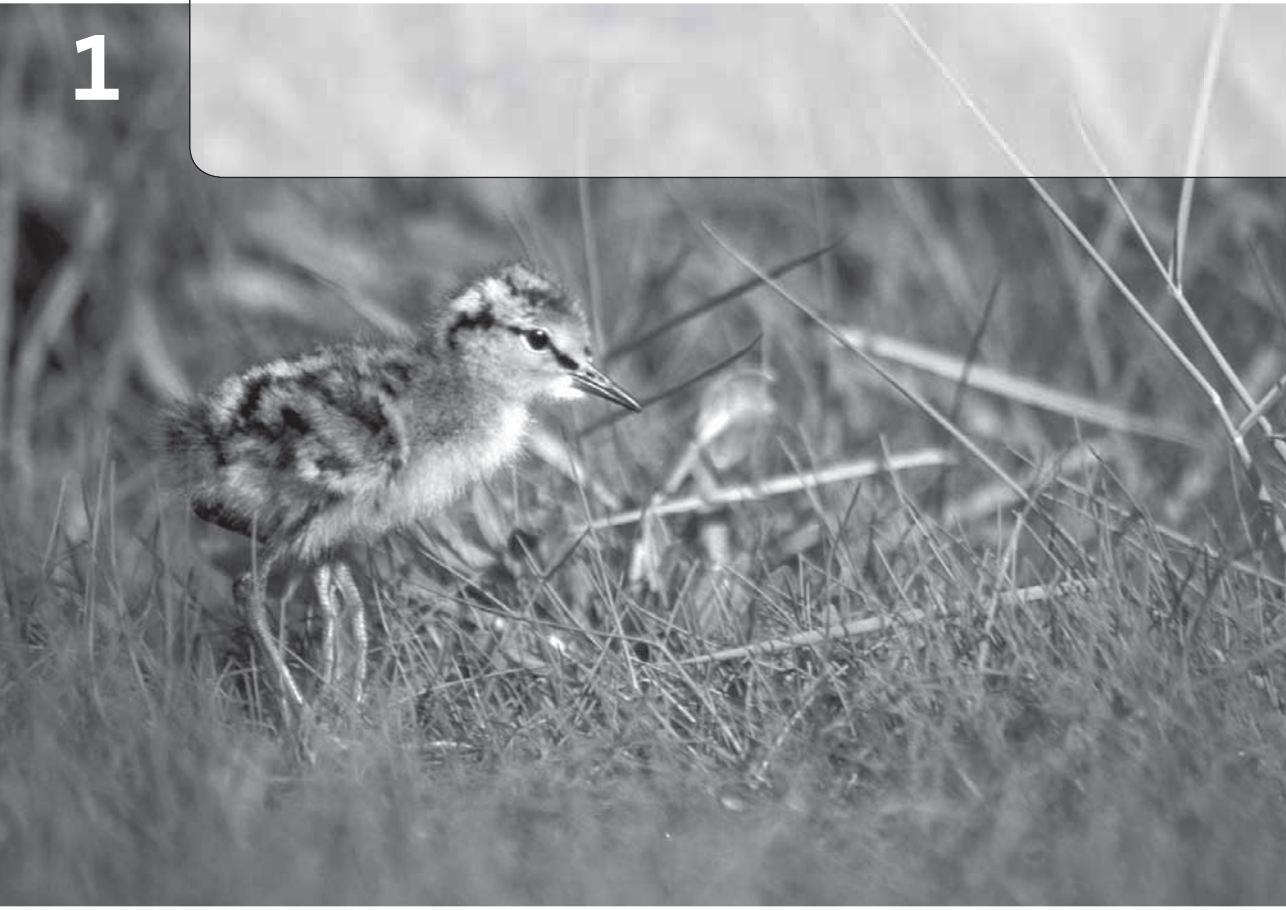


THE ALTRICIAL-PRECOCIAL SPECTRUM IN BIRDS

All birds have in common that their offspring hatch from eggs that develop outside the mother's body, but the structural and functional state in which young birds hatch varies enormously between species. When megapode chicks emerge from their egg, buried in warm soil or decomposing litter, they are fully feathered and capable of digging themselves to the surface, walking about, keeping warm and finding their own food without any help from their parents, and they can fly within a day. At the other extreme, the chicks of most songbirds, owls and parrots hatch without any feathers, with closed eyes and poorly developed muscles, and incapable of doing much more than raise their heads and beg for food when something (a parent?) arrives at the nest, swallow, and digest. They are almost totally dependent on their parents for staying warm, detecting predators, and food acquisition. They remain so for an extended period in which they stay in the nest and, for some aspects like feeding, even beyond. Many other bird species fall at varying points in between these two extremes, both with respect to the state of the chick at hatching and to the subsequent developmental trajectory. This diversity includes multiple anatomical and physiological traits, behaviour, and parent-offspring relationships. These traits partly vary independently of each other, but there is sufficient covariation among them to distinguish a single major axis of variation, which is known as the altricial-precocial spectrum (Nice 1962, Starck & Ricklefs 1998). Of the several classifications that have been proposed to subdivide this gradient, that of (Nice 1962) has become the most used (fig. 1.1).

Naturally, it is of great interest to understand the selective factors that have led to the evolution of the altricial-precocial spectrum. Projection of the current diversity of developmental modes onto hypotheses about the phylogeny of birds does not allow firm conclusions on the avian ancestral state, although it seems more likely that it was precocial than altricial (Starck & Ricklefs 1998). Whatever the case, the difference between the two major developmental modes must have arisen in one of the basic splits in the avian phylogeny. Evolutionary reversals have occurred at least once, and the 'middle ground' of the spectrum – represented by semialtricial and semiprecocial species – has probably been occupied from both fully altricial and fully precocial roots (Ricklefs & Starck 1998). However, most of these transitions have taken place early in the evolutionary diversification of birds. Developmental mode rarely varies within bird families and even less often within orders (the order Charadriiformes on which this thesis focuses forms an exception, see below). Apparently, it is an evolutionary conservative trait, "not a characteristic of birds that responds readily to environmental factors" (Ricklefs & Starck 1998). This does not mean that selection on developmental mode is nowadays absent or inconsequential. Rather, if it is hard to change a mode once it has become established in a lineage, this character may itself become a factor shaping the success of that lineage under different environmental conditions. Developmental mode may thus shape a bird group's ecological niche and evolutionary success by constraining choice of habitat, food type, or in other ways. Therefore, it is of interest to explore the ecological consequences of variation in developmental mode.

Although from a morphological-physiological point of view the most fundamental division along the altricial-precocial axis seems to be that between truly altricial (altricial-1) species and all other developmental groups (Starck & Ricklefs 1998), a major dividing point from a behavioural perspective is leaving the nest – so much that the term *nidifugous* (for chicks that leave the nest soon after hatching) is often equated with *precocial*, and *nidicolous* (for young that stay in the nest for some time) with *altricial*. The ability of the chicks to leave the nest, move around, hide upon alarm, or even follow the parents further away must have major consequences for predation risk and the economics of food acquisition of the family unit. According to Ricklefs & Starck (1998), the essence of this ability lies in the necessary neuromotor and sensory coordination in the higher centres of the chick's brain, and differences among nidifugous taxa reflect more the intensity of expression than the presence or absence of particular functional capabilities. From this point of view, semiprecocial birds can be seen as "precocials in which the parents gather food and deliver it to the chicks in a central place" (Ricklefs & Starck 1998). But while differences in demands on the functionality of various organ systems between young that merely wander about near the nest site and chicks that go out to find their own food may indeed be a matter of degree, in a broader ecological sense the division between parental feeding and self-feeding represents another major transition in the spectrum.

FIGURE 1.1. Nice's (1962) classification of the altricial-precocial spectrum, with major characteristics distinguishing the classes, and examples of bird families belonging to each.

Category	Plumage	Eyes	Nest attendance	Parental care	Examples
Precocial-1	contour feathers	open	leave nest area	none	megapodes
Precocial-2	down			brooding vigilance	ostriches, ducks & geese, plovers, sandpipers & allies
Precocial-3				food showing	pheasants, grouse, guineafowl
Precocial-4				feeding young	cranes, bustards, rails, grebes, divers, oystercatchers, murrelets
Semiprecocial			leave nest stay near		gulls & terns, many auks
Semialtricial-1			stay in nest		raptors, storks & herons, crab plover
Semialtricial-2		closed			pigeons, cormorants
Altricial	none				songbirds, parrots, gannets

SELF-FEEDING PRECOCIALITY

The period of provisioning food to growing young is generally seen as one of the most demanding stages in the life cycle of adult birds (Drent & Daan 1980, Weathers & Sullivan 1993). When parent birds do not have to spend energy and time on finding and transporting food to their young, this will reduce the associated 'cost of reproduction', with potentially important consequences for life-history trade-offs, and mating and parental care systems (Temrin & Tullberg 1995, Thomas & Szekely 2005). Simultaneously, the burden of finding food is shifted to the chick. It must leave the shelter of the nest and exert a high level of activity, which is very likely to increase its energy expenditure and reduce the amount of growth achieved per unit energy metabolised, compared to altricial nestlings. This redistribution of effort from parent to chicks proceeds gradually from taxa in which chicks follow their parents to be fed (precocial-4) or shown food (precocial-3) on the feeding grounds, via groups in which parents provide no food but do warm and guard the young (precocial-2), to the totally independent megapodes (precocial-1), but it remains to be seen whether these steps are all of the same magnitude in an energetic sense.

Some other potential consequences are particular to the self-feeding mode. First, the fact that incompletely developed chicks do not possess the same power and range of foraging skills that fully-grown and experienced adults have precludes certain food types (those requiring strength or intricate handling) and even entire habitats to be exploited as a food resource. For instance, self-feeding chicks do not forage in trees or at sea, hawk for aerial insects, dive deep for fish or benthic organisms, pry larvae from under bark or clams from their shells, or kill and eat other birds or mammals. Second, self-feeding chicks cannot fall back on their parents' abilities to ensure food acquisition during and after periods of unfavourable foraging conditions. This entails the risk that chicks end up in a negative spiral if a reduced nutritive condition affects their own foraging performance, and may render them particularly sensitive to short-term fluctuations in food availability.

Selection pressures operate on animals in their natural environment, and therefore need to be studied foremost in that natural environment. However, few studies have investigated how precocial chicks perform energetically, and what factors affect their performance in the field. For instance, over the past decades, energy expenditure and energy budgets have been studied in nestlings of several tens of bird species, but until recently these were mostly species in which young are fed by their parents (e.g. 28 out of 30 studies reviewed by Weathers (1992, 1996). Partly, this reflects the interest in brood energetics as a factor driving evolution of life history and parental decisions on reproductive investment that arose from the ideas of Lack (1968), Ricklefs (1974), and Drent & Daan (1980). But it also reflects the fact that it is difficult to make metabolic measurements on chicks under field conditions when they wander widely in search of food. The advent of the doubly-labelled water method (Lifson & McClintock 1966, Speakman 1997, Visser & Schekkerman 1999) has made this feasible, but it is still far less easy than when the chicks stay in a nest.

PRECOCIAL SHOREBIRDS

Shorebirds, also known as waders or Charadrii, are a morphologically well-defined but paraphyletic group within the order Charadriiformes. The two largest shorebird families, the Charadriidae (plovers and lapwings) and the Scolopacidae (snipes, sandpipers, godwits, curlews and phalaropes) both have mostly self-feeding chicks, that are guarded, led and brooded by one or both parents (del Hoyo *et al.* 1996). The snipes and woodcocks form an exception in that they feed their young, usually only for part of the prefledging period. The Scolopacidae form a clade together with self-feeding jacanas, seedsnipes and the Plains-wanderer *Pedionomus torquatus*, and with the painted-snipes that feed their chicks during the first week. This group as a whole is less closely related to the plovers than to a clade containing the parent-fed gulls, terns and auks, as well as the semialtricial Crab Plover *Dromas ardeola* and the coursers and pratincoles which feed their young only for a short time. The closest relatives of the plovers are the stilts and avocets, also with self-feeding chicks, and the semiprecocial oystercatchers that feed their young until well after fledging, with the semiprecocial and parent-fed thick-knees, sheathbills, and probably also the Magellanic Plover *Pluvianellus socialis* somewhat more distant (Paton *et al.* 2003, Thomas *et al.* 2004, van Tuinen *et al.* 2004). The Charadriiformes thus are an order with an uncharacteristically high diversity of developmental modes (Thomas & Szekely 2005).

The diet of self-feeding shorebird chicks generally consists of small invertebrates, taken from low vegetation, the surface of the soil or from the upper layers of mud or shallow water (del Hoyo *et al.* 1996). Although the chicks usually leave the nest within a day after hatching, they are rather thermolabile in comparison to other precocial bird groups like Anseriformes and Galliformes, because of a combination of relatively poor insulative properties of the natal down, a relatively low capacity for generating heat, and small size (Visser & Ricklefs 1993b). They are dependent on parental brooding to regularly restore their body temperature in outdoor conditions for some time (usually until one or two thirds into the prefledging period), and the time involved in this is

TABLE 1.1. Number of shorebird species in three groups differing in chick feeding mode, with predominantly arctic, temperate (including mountains in warm regions), and (sub)tropical breeding distribution (distributions from del Hoyo *et al.* 1996).

Group	Main breeding distribution			Total species
	arctic	temperate	(sub)tropical	
Shorebirds with parent-fed young[1]	2 (13%)	8 (53%)	5 (33%)	15
Shorebirds with partly parent-fed young[2]	2 (4%)	16 (31%)	34 (65%)	52
Shorebirds with entirely self-feeding young[3]	46 (31%)	54 (36%)	48 (32%)	148
Plovers and lapwings (Charadriidae)	7 (11%)	24 (36%)	35 (53%)	67
Snipes and sandpipers (Scolopacidae)	41 (48%)	35 (41%)	10 (12%)	86

1 Haematopidae, Chionidae, Pluvianellus, Dromas; 2 Burhinidae, Glareolidae, Rostratulidae, some Scolopacidae;
3 Jacanidae, Recurvirostridae, Charadriidae, Pedionomus, Thinocoridae, most Scolopacidae

largely lost as foraging time for the chick (Chappell 1980, Beintema & Visser 1989a, Visser & Ricklefs 1993a). As a consequence, food intake is sensitive to weather conditions that affect the chicks' cooling rate (notably temperature, wind and rain). This is bound to apply also for energy expenditure.

At first sight therefore, the developmental mode of shorebird chicks seems to be suited mainly to benign climatic conditions. Indeed, the highest diversity of plover species is found in tropical and warm-temperate (southern hemisphere) regions, possibly reflecting an evolutionary origin here (table 1.1). In contrast, the Scolopacidae show the highest species diversity in the boreal and arctic regions of the northern hemisphere. Shorebird species with a predominantly arctic breeding distribution are much more common among families with self-feeding young than among groups with parental feeding (table 1.1). This begs two questions: how do self-feeding arctic shorebird chicks cope with the thermal difficulties, and what makes the Arctic such an attractive breeding area despite these?

SHOREBIRDS AS MEADOW BIRDS

Evolutionary ecology is a scientifically interesting field in itself, but also provides a framework for addressing applied problems in nature management and conservation. In this thesis I look at shorebird chick development from both perspectives. The applied perspective concerns the role of growth and survival problems of chicks in the population declines shown by shorebirds breeding in agricultural grasslands in the Netherlands (fig. 1.2) and elsewhere in Europe.

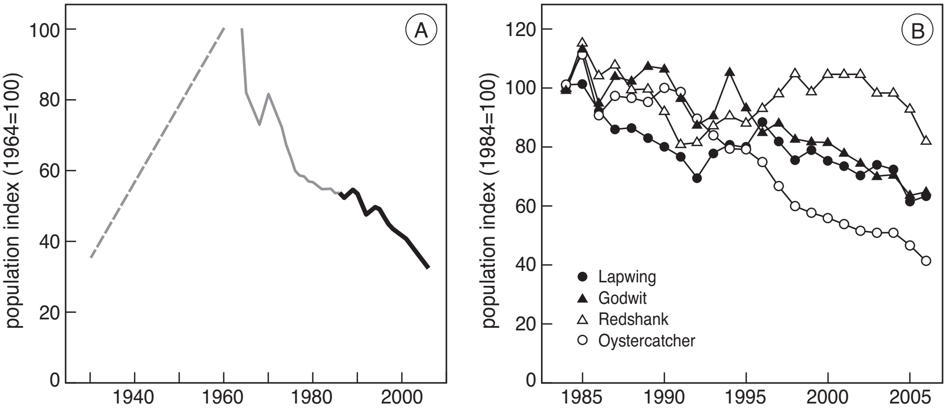
The landscape of the low-lying, western and northern parts of the Netherlands has been formed by sedimentation and transgression processes in the deltas of the rivers Rhine and Meuse, followed by centuries of human land reclamation and consolidation from 1,000 AD onwards. The resulting peat and clay-on-peat soils were prone to oxidise and subside when drained and have been used predominantly as grasslands for dairy farming since the 16th century (Beintema *et al.* 1995). In this man-made habitat, a characteristic community of breeding birds developed, of which shorebirds were a prominent part: Lapwing *Vanellus vanellus*, Common Snipe *Gallinago gallinago*, Black-tailed Godwit *Limosa limosa*, Common Redshank *Tringa totanus* and Ruff *Philomachus pugnax*. Besides shorebirds, several dabbling ducks (notably Mallard *A. platyrhynchos*, Shoveler *Anas clypeata* and Garganey *A. querquedula* and passerines (notably Skylark *Alauda arvensis*, Meadow Pipit *Anthus pratensis* and Yellow Wagtail *Motacilla flava)* and the Corncrake *Crex crex* were also part of this community (Beintema 1986).

From the early 20th century onwards, the agricultural use of these grasslands was increasingly intensified and this probably enhanced their suitability as breeding habitat for the larger shorebirds (Beintema *et al.* 1995, 1997). The adults of these species depend on a high availability of soil fauna (particularly earthworms) as food and this must have improved due to a combination of increasing fertiliser application and moderate drainage that reduced winter flooding but left the soil moist until late in the spring. Perhaps also aided by legal restrictions on hunting and egg-collecting, species like Northern Lapwing and Black-tailed Godwit strongly increased, and Oystercatcher

Haematopus ostralegus and Eurasian Curlew *Numenius arquata* colonised agricultural grasslands as a breeding habitat. The heydays for the Black-tailed Godwit were reached just before or around 1960, when ≥125 000 pairs were estimated to breed in the Netherlands (Mulder 1972, Bijlsma *et al.* 2001), which had thus become the country holding by far the largest part of the European population of the nominate subspecies *L. l. limosa*.

By that time, the smaller shorebirds were already declining and this was soon followed by strong declines in the Black-tailed Godwit, and the other large species (fig. 1.2). Besides a direct loss of grassland area mainly due to urbanisation and road-building, degradation of the quality of the remaining habitat played a major role in these declines. The period 1945-1980 saw rapid agricultural change involving widespread land consolidation and intensive drainage, fertilisation and mechanisation allowing increases in stocking densities and earlier, more frequent and faster mowing of grass. In the 1990s the total number of livestock equivalents per ha of grassland, probably a good metric for the overall intensity of agricultural production, in the Netherlands was the highest of all European countries and four times the EU average (at more than 4 le/ha). Livestock numbers and fertiliser use have declined slightly since *c.* 1990 in response to EU measures aimed at reducing overproduction and environmental problems with manure. However, some aspects of intensification have continued, including earlier and more rapid mowing in spring and extensive reseeding of grassland with productive grass monocultures. Shorebirds and other meadow birds were negatively affected by these changes mainly because agricultural land use increasingly

FIGURE 1.2. A: Population development of Black-tailed Godwit in the Netherlands since the early 20th century. Broken line 1930-1960 based on scant density information in Bijlsma *et al.* 2001, grey line 1964-1984 based on counts in a limited number of sites (SOVON 2002), black line from 1984 onwards on a national monitoring network for meadowbirds (Netwerk Ecologische Monitoring, SOVON & CBS). B: Population development of Northern Lapwing, Black-tailed Godwit, Common Redshank and Eurasian Oystercatcher in farmland (NEM, SOVON & CBS; Teunissen & Soldaat 2006).



interfered with their breeding cycle, reducing reproductive success. The smaller species suffered first, as they are more sensitive to reductions in breeding success, breed later in the spring, and some are also more sensitive to drainage than the larger ones (Beintema *et al.* 1995). Ruff, Snipe and Corncrake have almost completely disappeared from agricultural grasslands, and only hang on in reserves.

MEADOW BIRD CONSERVATION AND RESEARCH

These declines did not go unnoticed and since the early 1960s conservation of meadow birds has been on the agenda of the Dutch government and non-governmental organisations. Initially, most effort was put into the creation of reserves managed especially for meadow birds or a combination of birds and botanical values. In 1975, the ‘Relatienota’ introduced the concept of agri-environment schemes (management contracts) to also protect populations in conventional farmland. Farmers were reimbursed financially for a less intensive land use that should improve breeding conditions for meadow birds. After a slow initial uptake, the area under contract increased strongly from the late 1980s onward, and the variety of contracts forms also increased. Early schemes consisted mainly of a disturbance-free period, in which no agricultural activity including grazing or mowing is allowed, from 1 April until varying dates into the spring (e.g. 23 May, 1, 8 or 15 June etc), imposed on individual fields within predefined search areas with reasonably high meadow bird densities. In the 1990s, the spatial restrictions were reduced and contracts for ‘active nest protection’ (i.e. marking shorebird clutches and avoiding them during farming operations, Musters *et al.* 2001), were added. Recently, schemes have been implemented in which collectives of farmers apply a variety of measures, spatially coordinated at the area level. In 2005, agri-environment schemes covered *c.* 150,000 ha of Dutch grassland, of which 27,000 ha includes restrictions on field use and 123,000 ha nest protection. An additional 200,000 ha is covered by an unpaid nest protection scheme involving volunteers to search and mark clutches (van Paassen 2006). However, all this has so far not resulted in a reversal of the downward population trends of meadow birds. Several species have even showed an accelerated decline in recent years (Teunissen & Soldaat 2006, Teunissen 2007; fig. 1.2).

With the advent of conservation measures in the 1960s, research on grassland shorebirds also increased, mainly directed at their conservation needs. Initially, this involved mainly censuses and correlative work on habitat associations. In the 1970s and early 1980s a large body of research focused on factors affecting clutch survival, as it became evident that early mowing and high density grazing caused the loss of many meadow bird clutches (Beintema & Müskens 1987, Kruk *et al.* 1996). This work provided the basis under the agri-environment schemes that postpone mowing, and under the program of active nest protection by volunteers and farmers. The latter already had a long history in Friesland, tightly linked to a tradition of collecting lapwing eggs.

In the mid-1970s Albert Beintema initiated studies on the ecology of chicks of grassland shorebirds, involving work on growth rates (Beintema & Visser 1989b, Beintema 1994), foraging-brooding time budgets (Beintema & Visser 1989a), leading to studies on the development of temperature regulation in precocial chicks by Henk Visser (1991), and chick diets (Beintema *et al.* 1991). This work showed that young chicks are sensitive to weather conditions because of limitations on foraging time set by their need for parental brooding, and suggested that older chicks may run into problems if they have to subsist on small prey items. This might have become difficult in modern grasslands, as Siepel (1990) reported that increasing fertiliser use leads to a smaller average size of grassland invertebrates, and as drainage could have reduced the availability of soil fauna that might provide a source of larger prey items for older chicks (Beintema *et al.* 1991). These results prompted the study that forms the basis of this thesis, focusing on how agricultural grassland use affects the availability of invertebrate food for chicks of Black-tailed Godwit and Northern Lapwing, and how this management-mediated food availability interacts with weather-mediated time budgets to determine their food intake, growth rate and survival (Schekkerman 1997). Because of the international importance of the Dutch breeding population and the fact that it is still widespread but rapidly in decline, recent research and conservation efforts have concentrated on the Black-tailed Godwit, a species that has recently been red-listed as globally near-threatened by IUCN (2007).

In 2001, Kleijn *et al.* published a study into the effectiveness of of agri-environment schemes employed in Dutch grasslands in the influential journal *Nature*. Fields with agri-environment contracts (involving mainly postponed mowing of individual fields) did not show higher breeding densities of grassland shorebirds than nearby fields without, and numbers of foraging birds were even lower on the former. The study triggered two important developments. First, it highlighted the need for scientifically sound evaluation of agri-environment schemes, which had largely been lacking until that time (Kleijn & Sutherland 2003). Several subsequent studies supported the initial conclusion that the effectiveness of existing schemes seems to be very limited (Kleijn & van Zuijlen 2004, Willems *et al.* 2004, Verhulst *et al.* 2007). Some species, notably Lapwings, even responded negatively to scheme instalment. Secondly, these findings accelerated the already initiated development of more comprehensive and more spatially coherent forms of agri-environment management, among which 'mosaic management'.

RESEARCH APPROACH

All studies into the effectiveness of agri-environment schemes for meadowbirds to date have measured breeding density as the response variable. Although this metric corresponds to the schemes' goal of increasing population size, it tells us very little about the mechanisms underlying the observed response. This 'black box approach' has two important limitations. First, density effects can be confounded by dispersal in addition to local breeding success, and this might lead to erroneous conclusions. If a scheme increases reproductive success but the produced fledglings settle outside their native area, management is beneficial to the wider population even if local densities remain unchanged. On the other hand, it is also possible that management increases a site's attractiveness to settling birds, but breeding success there is too low to compensate adult mortality, so that the managed areas remain ‘population sinks’. In such a case the management would erroneously be considered effective on the basis of density changes alone.

Second, an understanding of the mechanisms through which environmental conditions affect the performance of local breeding birds can be used to improve conservation management, by identifying features and components that do and that do not function as intended in their design, and by highlighting limiting factors that need to be alleviated. For instance, if narrow field margins that are left uncut, to provide godwit chicks with a refuge during cutting and a minimum of feeding habitat in the period thereafter, are not actually used by broods, they could be subsidised only if made wider so that they do become attractive (Schekkerman & Müskens 2001). Also, for some management measures, like these refuge strips, it is in practice very difficult to test their effectiveness via a numeric response, as they are usually applied in combination with other measures. Although measuring changes in breeding density remains a useful tool to evaluate policy and management, it is thus important to augment this with research revealing the demographic drivers behind population change and with more detailed studies into the way in which animals depend on their environment. In the papers contained in this thesis, I have adopted this mechanistic approach to study relationships between environmental conditions and the performance of shorebird chicks.

Figure 1.3 provides a general hypothesis of the way in which growth and survival of young grassland shorebirds may be influenced by these conditions, including weather, agricultural use and predation pressure. Chicks growing up in natural habitats like arctic tundra are subject to much the same influences, although these habitats are not directly managed by humans and some of the factors shown (like grassland use) do not apply there. A chick’s growth rate is determined by the balance between its energy intake and energy expenditure. Energy expenditure is affected mainly by body size (through basal metabolic rate), weather conditions (thermoregulation) and foraging time (activity costs). Energy intake is the product of foraging time and foraging success, which may be influenced by weather (through brooding time and availability of grassland invertebrates) and farming practice (through abundance of invertebrates). In contrast to some other bird groups like many seabirds, growing shorebird chicks do not accumulate substantial deposits of fat that can be mobilised in periods of negative energy balance (Chapter 2). Therefore a chick’s nutritive condition can be defined as its body mass relative to the mass expected at its age. If chicks consistently grow slower than normal, they will eventually die when they fall below a critical condition level (starvation). Already before this level is reached, a reduced condition may increase mortality through a higher vulnerability to predators (caused by a slower escape response or an increase in risk-taking to maximise food intake). Predation risk may thus be determined by the chick’s state as well as by the abundance of predators in the landscape, and may be further affected by habitat features like the availability of cover, which relate to management. Finally, grassland use, particularly mowing, also causes direct mortality (fig. 1.3). There may also be non-lethal fitness consequences of poor nutrition that become apparent only later in life (Gebhard-Henrich & Richner 1998), but these are not addressed in this thesis.

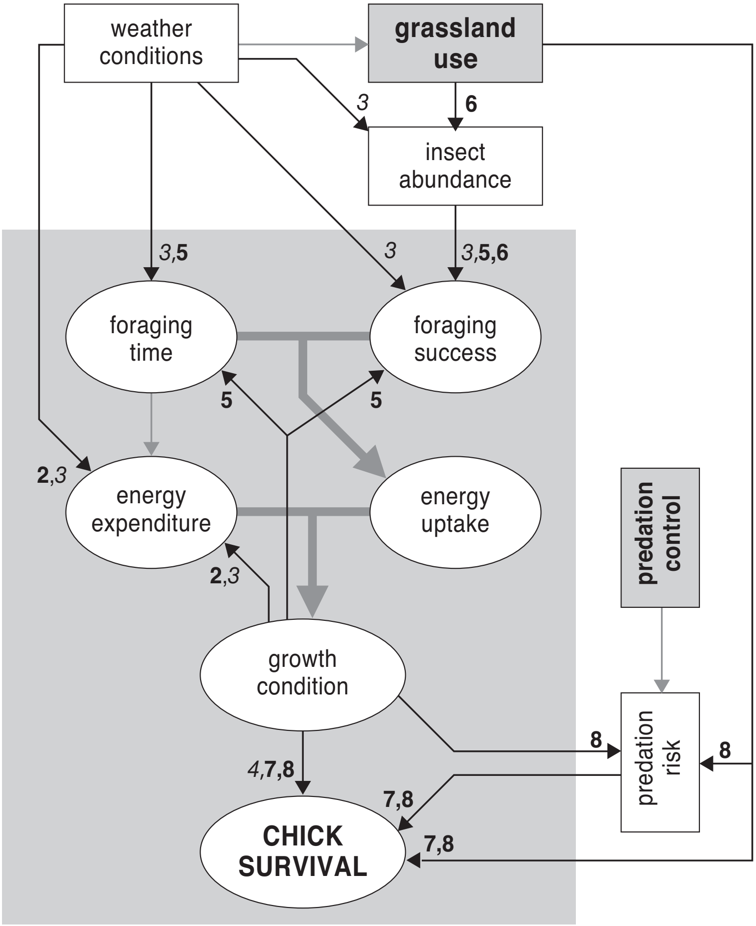


FIGURE 1.3. Schematic representation of (hypothetical) relationships between environmental conditions (weather, farming and predation) and the growth and survival of grassland shorebird chicks (represented by the shaded rectangle). Thin black arrows denote relationships studied in this thesis (chapters indicated by numbers); thick grey arrows relationships that can be derived from first principles. For chicks of arctic-breeding shorebirds (chapter indications italic, not bold), management by humans (grassland use and predation control) does not apply.

OUTLINE OF THE THESIS

Chapter 2 starts off with the question what are the energetic consequences (for the chicks) of the shift of food provisioning from parents to self-feeding young. Energy budgets of growing chicks of Black-tailed Godwit and Northern Lapwing are constructed on the basis of field and laboratory measurements. These show that overall amount of energy metabolised over the prefledging period is considerably higher than in typical parent-fed birds, and that this is mainly due to high expenditure on thermoregulation and activity. In chapter 3, similar measurements made in the Red Knot *Calidris canutus* confirm the idea that energy requirements are even higher when a chick has to find food and grow up in the much colder conditions of the arctic tundra. By investigating relationships between weather, availability of invertebrate food, time budgets and growth rate, this chapter also addresses the question how Red Knot chicks overcome the energetic difficulties imposed by the arctic climate.

What ultimately matters is not growth rate but survival of chicks to fledging (and beyond), but measuring this is not an easy task in nidifugous broods that behave cryptically and may move over considerable distances. Fortunately, many arctic-breeding shorebirds migrate to areas where they can be more easily accessed by researchers. In chapter 4 we investigate the effects of annual variation in weather conditions in the Siberian tundra on the proportion juveniles among Curlew Sandpipers *Calidris ferruginea* 'wintering' in South Africa.

Chapter 5 returns to temperate grasslands, and describes how foraging time, foraging success and prey size develop with age in chicks of the Black-tailed Godwit. It also investigates the effect of weather conditions on foraging time and foraging success. Chapter 6 then compares the abundance of vegetation-dwelling invertebrates, and the intake rates of godwit chicks that feed on them, between such a meadowbird reserve and grasslands used for conventional, intensive dairy-farming. The results provide evidence for a negative long-term effect of intensive farming on invertebrate populations, but much more strongly so for a short-term effect caused by cutting of the vegetation. The reduction in intake rate shown by godwit chicks foraging in cut agricultural fields was sufficiently large to jeopardise their growth, suggesting that postponing the first cut could be an effective measure to increase chick survival. However, in the observational setup of these studies, we were unable to actually compare chick survival between management treatments, not in the least because broods actively selected to stay in uncut fields.

In the mid-1990s, estimates of survival of meadow bird chicks, and hence of reproductive success as a whole (chicks fledged per breeding pair), were very scarce in the Netherlands. Site- or year- specific chick survival estimates require following the fate of individually recognisable broods. This can be done by colour-marking the adults (Buker & Winkelman 1987, Kruk *et al.* 1997, Groen & Hemerik 2002), but radiotelemetry provides a more efficient method (Schekkerman & Müskens 2000), and if chicks are radio-tagged as well, allows determining the causes of chick deaths. Chapters 7 and 8 describe the results of such studies conducted in 2002-2005 (see also Schekkerman *et al.* 2005, Teunissen *et al.* 2005).

In chapter 7, the effectiveness of a newly developed agri-environment scheme is evaluated by comparing reproductive success of Black-tailed Godwits between managed sites and nearby, paired control sites. The results indicate that chick survival is higher when more uncut grassland is available, but reproductive success in most of the managed sites remained below the level required for a self-sustaining population. Comparison of our estimates with earlier studies suggests that godwit chick survival has declined considerably over recent decades, and is a major driver of this species' population decline. Chapter 8 presents a closer investigation of the causes of death of godwit and lapwing chicks, as observed in the mosaic management study and a simultaneous study into predation on meadow birds. We analyse whether radio-tagging negatively affects the survival of chicks, and quantify the relative importance of different mortality factors, including interactions between predation and agricultural practice.

In chapter 9, I draw together the results described in the previous chapters and other published studies, returning to the points raised in this introduction, and discussing the outlook for preserving populations of Black-tailed Godwit and other meadowbirds in Dutch farmland.

REFERENCES

- Beintema A.J. 1986. Man-made polders in The Netherlands: a traditional habitat for shorebirds. Colonial Waterbirds 9: 196-202.
- Beintema A.J. & G.J.D.M. Müskens 1987. Nesting success of birds breeding in Dutch agricultural grasslands. Journal of Applied Ecology 24: 743-758.
- Beintema A.J. & G.H. Visser 1989a. The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77: 181-192.
- Beintema A.J. & G.H. Visser 1989b. Growth-parameters in chicks of Charadriiform birds. Ardea 77: 169-180.
- Beintema A.J., J.B. Thissen, D. Tensen & G.H. Visser 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. Ardea 79: 31-43.
- Beintema A.J. 1994. Condition indices for wader chicks derived from body-weight and bill-length. Bird Study 41: 68-75.
- Beintema A.J., O. Moedt & D. Ellinger 1995. Ecologische atlas van de Nederlandse weidevogels. Schuyt & Co, Haarlem.
- Beintema A.J., E. Dunn & D. Stroud 1997. Birds and wet grasslands. In: D.J. Pain & M.D. Pienkowski (eds.) Farming and birds in Europe: the Common Agricultural Policy and its implications for bird conservation: 269-296. Academic Press, San Diego.
- Bijlsma R., F. Hustings & C.J. Camphuysen 2001. Common and scarce birds of The Netherlands. Avifauna of The Netherlands 2. GMB / KNNV, Haarlem.
- Buker J.B. & J.E. Winkelman 1987. Eerste resultaten van een onderzoek naar de broedbiologie en het terreingebruik van de grutto in relatie tot het graslandbeheer. DBL-rapport 12, Dienst Beheer Landbouwgronden, Utrecht.
- Chappell M.A. 1980. Thermal energetics of chicks of arctic-breeding shorebirds. Comparative Biochemistry and Physiology 65A: 311-317.
- del Hoyo J., A. Elliot & J. Sargatal 1996. Handbook of the birds of the world. Vol 3. Hoatzin to Auks. Lynx Edicions, Barcelona.
- Drent R.H. & S. Daan 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.
- Gebhard-Henrich S. & H. Richner 1998. Causes of growth variation and its consequences for fitness. In: J.M. Starck & R.E. Ricklefs (eds.) Avian growth and development: 324-339. Oxford University Press, New York.
- Groen N.M. & L. Hemerik 2002. Reproductive success and survival of black-tailed godwits *Limosa limosa* in a declining local population in The Netherlands. Ardea 90: 239-248.
- Kleijn D., F. Berendse, R. Smit & N. Gilissen 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413: 723-725.
- Kleijn D. & W.J. Sutherland 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? Journal of Applied Ecology 40: 947-969.
- Kleijn D. & G.J.C. van Zuijlen 2004. The conservation effects of meadow bird agreements on farmland in Zeeland, The Netherlands, in the period 1989-1995. Biological Conservation 117: 443-451.
- Kruk M., M.A.W. Noordervliet & W.J. ter Keurs 1996. Hatching dates of waders and mowing dates in intensively exploited grassland areas in different years. Biological Conservation 77: 213-218.

- Kruk M., M.A.W. Noordervliet & W.J. ter Keurs 1997. Survival of black-tailed godwit chicks *Limosa limosa* in intensively exploited grassland areas in The Netherlands. Biological Conservation 80: 127-133.
- Lack D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Lifson N. & R. McClintock 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. Journal of Theoretical Biology 12: 46-74.
- Mulder T. 1972. De Grutto in Nederland. Wetenschappelijke Mededeling nr. 90, KNNV, Hoogwoud.
- Musters C.J.M., M. Kruk, H.J. de Graaf & W.J. ter Keurs 2001. Breeding birds as a farm product. Conservation Biology 15: 363-369.
- Nice M.M. 1962. Development of behavior in precocial birds. Transactions of the Linnean Society, New York 8: 1-211.
- van Paassen A.G. 2006. Vrijwillige weidevogelbescherming in Nederland 1993-2004. De Levende Natuur 107: 104-107.
- Ricklefs R.E. 1974. Energetics of reproduction in birds. In: R.A. Paynter (ed.) Avian Energetics No. 15. Nuttal Ornithological Club, Cambridge.
- Ricklefs R.E. & J.M. Starck 1998. The evolution of the developmental mode in birds. In: J.M. Starck & R.E. Ricklefs (eds.) Avian postnatal development: 366-380. Oxford University Press, New York.
- Schekkerman H. 1997. Graslandbeheer en groeimogelijkheden voor weidevogelkuikens. IBN-rapport 292, DLO Instituut voor Bos- en Natuuronderzoek, Wageningen.
- Schekkerman H. & G. Müskens 2000. Produceren Grutto's *Limosa limosa* in agrarisch grasland voldoende jongen voor een duurzame populatie? Limosa 73: 121-134.
- Schekkerman H. & G.J.D.M. Müskens 2001. 'Vluchtstroken' als instrument in agrarisch weidevogelbeheer. Alterra-rapport 220, Alterra, Wageningen.
- Schekkerman H., W. Teunissen & E. Oosterveld 2005. Broedsucces van grutto's bij agrarisch mozaïekbeheer in 'Nederland Gruttoland'. Alterra-rapport 1291, Alterra, Wageningen.
- Siepel H. 1990. The influence of management on food size in the menu of insectivorous animals. Proceedings in Experimental and Applied Entomology, N.E.V. Amsterdam 1: 69-74.
- SOVON 2002. Atlas van de Nederlandse broedvogels 1998-2000. Nationaal Natuurhistorisch Museum Naturalis, Leiden.
- Speakman J.R. 1997. Doubly Labelled Water. Theory and practice. Chapman and Hall, London.
- Starck J.M. & R.E. Ricklefs 1998. Patterns of development: the altricial-precocial spectrum. In: J.M. Starck & R.E. Ricklefs (eds.) Avian growth and development: 3-31. Oxford University Press, New York.
- Temrin H. & B.S. Tullberg 1995. A phylogenetic analysis of the evolution of avian mating systems in relation to altricial and precocial young. Behavioral Ecology 6: 296-307.
- Teunissen W. 2007. Afname van weidevogels versnelt sinds eeuwwisseling. SOVON-nieuws 20: 15-17.
- Teunissen W.A., H. Schekkerman & F. Willems 2005. Predatie bij weidevogels. SOVON-onderzoeksrapport 2005/11, SOVON, Beek-Ubbergen.
- Teunissen W.A. & L.L. Soldaat 2006. Recente aantalsontwikkeling van weidevogels in Nederland. De Levende Natuur 107: 70-74.

- Thomas G.H. & T. Szekely 2005. Evolutionary pathways in shorebird breeding systems: sexual conflict, parental care, and chick development. Evolution 59: 2222-2230.
- Verhulst J., D. Kleijn & F. Berendse 2007. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. Journal of Applied Ecology 44: 70-80.
- Visser G.H. 1991. Development of metabolism and temperature regulation in precocial birds. PhD Thesis, University of Utrecht.
- Visser G.H. & R.E. Ricklefs 1993a. Development of temperature regulation in shorebirds. Physiological Zoology 66: 771-792.
- Visser, G.H. & R.E. Ricklefs 1993b. Temperature regulation in neonates of shorebirds. Auk 110: 445-457.
- Visser G.H. & H. Schekkerman 1999. Validation of the doubly labeled water method in growing precocial birds: The importance of assumptions concerning evaporative water loss. Physiological & Biochemical Zoology 72: 740-749.
- Weathers W.W. & K.A. Sullivan 1993. Seasonal patterns of time and energy allocation by birds. Physiological Zoology 66: 511-536.
- Willems F., A. Breeuwer, R. Foppen, W. Teunissen, H. Schekkerman, P. Goedhart, D. Kleijn & F. Berendse 2004. Evaluatie agrarisch natuurbeheer: effecten op weidevogeldichtheden. SOVON-onderzoeksrapport 2004/02, SOVON /WUR /Alterra, Beek-Ubbergen.

Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development

2

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ABSTRACT

1. Understanding the ecological consequences of avian developmental modes requires knowledge of the energy requirements of chicks of different positions in the precocial-altricial spectrum, but these have rarely been measured in birds with self-feeding precocial young. We studied prefledging energy budgets in chicks of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus*, in the field and in the laboratory.

2. Lapwings show slower growth than godwits, reaching a 29% lower fledging mass (142 *vs.* 201 g) in a 32% longer period (33 *vs.* 25 days). Daily Energy Expenditure (DEE), measured by the doubly labelled water (DLW) technique, and daily Metabolised Energy (DEE plus energy deposited into tissue) increased proportionally to body mass at similar levels in both species.

3. Total Metabolised Energy (TME) over the fledging period was 8331 kJ in godwits and 6982 kJ in lapwings, 39% and 29% higher than an allometric prediction (Weathers 1992). Energy costs of activity and thermoregulation made up 50-53% of TME in the shorebirds, more than twice as much as in seven parent-fed species for which DLW-based energy budgets are available. In captive lapwings and godwits growing up under favourable thermal conditions with food readily accessible, these costs were 53-58% lower, and TME 26-31 % lower, than in free-living chicks.

4. This suggests that self-feeding precocial chicks have high energy requirements compared with parent-fed species, due to the costs associated with foraging. The proportion of TME allocated to tissue formation (13-15% deposited as tissue plus 10-12% synthesis costs) was low in the shorebirds, and reductions in food intake may therefore sooner lead to stagnation of growth than in parent-fed chicks. Furthermore, the need to forage limits the potential for saving energy by reducing activity in periods of food scarcity, as this will further decrease food intake.

5. Self-feeding precocial chicks thus seem to operate within fairly narrow energetic margins. At the same time, self-feeding may allow birds to utilise food types that could not be profitably harvested if they had to be transported to the young.

INTRODUCTION

Over the past decades, energy expenditure and energy budgets of nestling birds have been studied in a few tens of species (reviewed by Drent *et al*. 1992, Weathers 1992, 1996). Interest in this field was spurred by the idea that brood size and growth rate can be seen as reproductive strategies, shaped by selection pressures such as predation risk and the amount of food that parent birds can deliver to their young (Lack 1968, Ricklefs 1974, Drent & Daan 1980). Perhaps as a result, the great majority of studies of prefledging energy budgets have been conducted on species in which the young are fed by their parents (e.g. 28 out of 30 studies reviewed by Weathers 1992), and very few on birds with self-feeding young. An additional reason for the scarcity of studies on self-feeding precocials is that making the necessary measurements in the field is difficult due to their mobility.

Nevertheless, knowledge of the energetic requirements of precocial chicks may help understand the ecological consequences of different developmental modes in the precocial-altricial spectrum (Nice 1962, Ricklefs & Starck 1998). From an energetic viewpoint, the dichotomy between parent-fed and self-feeding young may be a particularly important distinction within this spectrum. Energy expenditure of parent birds raising self-feeding young may be lower than that of birds that feed their offspring. At the same time, the burden of collecting the necessary food is shifted to the chick. This calls for an active and exposed lifestyle that can be expected to result in high energy expenditure on activity and thermoregulation. Although self-feeding precocials tend to grow at a slower rate than (semi)altricials (Ricklefs 1973, Ricklefs *et al*. 1998), and this reduces energy requirements, the savings may be limited because tissue formation is only one of several components in the budget. The net result for total energy requirements is as yet hard to judge, because the necessary measurements are lacking. If foraging leads to high energy expenditure, the scope for underestimation in laboratory studies, where food is often readily available and chicks are sheltered from adverse weather, will be particularly large in self-feeding chicks. Therefore, it is important to study energy expenditure under field conditons.

We measured energy metabolism during the prefledging period in two shorebirds (Charadrii) with self-feeding chicks, Northern Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa*. In this paper, measurements obtained in the field and in the laboratory are compared, and prefledging energy expenditure and energy budgets are compared with those of species with parent-fed young.

METHODS

Study species

Black-tailed Godwit and Northern Lapwing breed in a wide belt across temperate Europe and western Asia, the latitudinal range being smaller in godwits (45-62°N) than in lapwings (36-67°N). At present, most of the European populations breed in agricultural lowland wet grasslands, where densities are often higher than in the original habitat, moist natural grasslands (Hagemeijer & Blair 1997). The young feed themselves from hatching onwards, but both parents or one (some lapwings are polygynous) stay with the brood until after fledging. Godwit broods show a clear preference for tall swards (20-50 cm high) where they take small arthropods from the vegetation. Lapwings are more often found on short (mown or grazed) swards, and on the banks of pools and ditches, where small invertebrates are taken from the soil surface and vegetation (Beintema *et al.* 1991).

Field study

Both species were studied in an area of agricultural and reserve grasslands with moderately low farming intensity near Baarn in The Netherlands (52°12'N, 5°19'E), in 1993-1995. Measurements of daily energy expenditure (DEE, kJ/d) were made using the doubly labelled water (DLW) method (Lifson & McClintock 1966, Nagy 1980, Speakman 1997, Visser & Schekkerman 1999). One or two chicks out of broods of three or four were captured, weighed and injected intraperitoneally with 0.1 to 0.4 ml (depending on body mass) of doubly labelled water (DLW) consisting of 31.1 atom-% ^{2}H and 62.7 atom-% ^{18}O. After an equilibration period of 1 h, four to six 10-15 µl blood samples were collected from veins in the leg (small chicks) or wing (larger ones) into glass capillary tubes, which were flame-sealed within minutes. Chicks were then released back to their family unit, and recaptured after 21.5-28.5 h (mean 24.2±1.2 h), to take a second set of blood samples and determine mass change. In a small number of chicks, blood samples were also collected before injection with DLW, in order to record background isotope levels.

Broods of Black-tailed Godwits are highly mobile and may show displacements of >1 km in a day (H. Schekkerman unpubl.), while the chicks are hard to find in the tall grass. Especially at high brood densities, this complicates recaptures. Therefore, most measurements on godwits were made on broods confined to enclosures of 0.4-0.6 ha, fenced with 0.5 m high wire-netting which allowed the parents but not the chicks to freely leave and enter (*cf.* Beintema and Visser 1989b, Chapter 5). Water but no food was provided within the enclosures, and the chicks foraged on arthropods occurring naturally in the vegetation. Enclosures were placed in preferred brood habitat (unmown reserve grassland), and their size was similar to the area available to wild broods at maximum observed densities in this habitat (1.7 broods/ha, H. Schekkerman unpubl.). Behaviour of enclosed godwits closely resembled that of free-living birds. Six measurements were made on free-ranging godwit chicks. Because Northern Lapwing broods are less mobile and more easily recaptured than those of godwits, all measurements were made on free-ranging young.

Weather conditions were recorded in the study area and logged every two minutes on a datalogger. Wind speed (m/s) was measured with a calibrated anemometer at 3 m above the ground. An approximation of the operative environmental temperature (T_e, °C) at chick level, which integrates air temperature and the heating effect of radiation (Bakken *et al.* 1985, Walsberg and Weathers 1986), was measured in a blackened copper sphere of 4 cm diameter placed 10 cm above the ground. Occurrence and duration of rainfall were recorded daily.

DLW analysis

$^2H/^1H$ and $^{18}O/^{16}O$ ratios in the blood samples were analysed with a SIRA 9 isotope ratio mass spectrometer at the Centre for Isotope Research, following procedures described in Visser & Schekkerman (1999). Analyses were done in duplicate, and a third capillary was analysed if the two measurements differed by more than 2%. Background concentrations were 0.0152 ± 0.00010 atom-% for ^2H and 0.2000 ± 0.00009 atom-% for ^{18}O (both N=6). We calculated CO_2-production (rCO_2, l/d) according to equation 34 in Lifson & McClintock (1966), with fractionation factors k_o and k_d taken from Speakman (1997), and a value of 0.13 for the fraction of water loss occurring by evaporation:

$$rCO_2\,(L/d) = (N / 2.078 \times (k_o - k_d) - 0.13 \times 0.0249 \times N \times k_d) \times 22.4,$$

in which N is the size of the body water pool (mol). This equation was derived by validating 11 DLW measurements in Northern Lapwing and Black-tailed Godwit chicks against respiration gas analysis in the laboratory (Visser & Schekkerman 1999). Relative errors of individual measurements ranged from -13% to +16%, with a mean of 0%, and showed no relationship with relative growth rate of the chick during the experiment (range -17 to +15%/d). These results indicate that the DLW method is applicable in shorebird chicks at a wide range of growth rates.

Because some injected isotope was sometimes lost by leakage through the puncture hole in the chicks' skin, N was not estimated from isotope dilution but from the relationship between percentage water content and the fraction of adult mass attained, derived from a sample of freshly dead chicks (see carcass analysis). DEE was calculated from rCO_2 using an energy equivalent of 27.33 kJ/l CO_2 (Gessaman & Nagy 1988). Water fluxes were calculated using equation 6 of Visser & Schekkerman (1999).

Laboratory trials

In 1986-1989, fresh eggs were obtained from breeding areas in the Netherlands and transported to the laboratory at Utrecht, where they were incubated at 37.5°C and 55-60% relative humidity. After hatching, chicks were housed in pairs in wooden boxes (45 × 60 cm) in a large climatic chamber at 20°C (light:dark 8:6, similar to outdoor conditions). Water and food were provided *ad libitum*, while extra heat was provided by a 100 W infrared lamp in a corner of each box. At 1-2 weeks of age, the chicks were housed in an outdoor aviary connected with an indoor section where heat (infrared lamp), water and food were provided. Chicks were fed a pellet diet containing 28.5% crude protein. Measurements of oxygen consumption were made regularly on the chicks in order to describe the development of thermoregulation (Visser & Ricklefs 1993a, b).

During measurements of Metabolisable Energy Intake (MEI, kJ/d) chicks were housed in pairs in wooden boxes as described above (housing chicks alone led to aberrant behaviour and retarded growth). Food intake was measured over 24 h intervals by weighing the food tray and correcting for water loss. Energy content of the food was determined by bomb calorimetry, and was 19.48 ± 0.019 kJ/g dry mass (N=4). At the end of each trial, we carefully collected and separated spilled food and faeces. Spilled food was weighed immediately. The faecal fraction was dried for 24 h at 60°C, and weighed. Energy content of faeces samples (*c.* 0.5 g) was determined by bomb calorimetry. Digestive efficiency for food pellets was 69.6 ± 2.59% (N=19) in godwits and 55.4 ± 1.71% (N=11) in lapwings, and was unrelated to chick age. These values were used to convert crude food intake to MEI.

Carcass analysis

Water content and energy density of growing chicks were determined by analysing the composition of carcasses of five Black-tailed Godwits and three Northern Lapwings of varying ages. The chicks were killed by predators or by accident in the field (N=5) or in the laboratory (N=3), but had not died of starvation. Their fresh mass spanned the range found in chicks of these species, up to fledging at 70-80% of adult mass (Beintema & Visser 1989a). Carcasses were weighed fresh and stored in a freezer for variable periods. After thawing, they were cut into parts and dried to constant weight at 60°C to obtain dry mass. Water content (%) was calculated as 100 × (fresh mass - dry mass) / fresh mass. Soluble fat was extracted in petroleum ether during 24h in a Soxhlet apparatus. Remains were dried for 24 h at 60°C to obtain lean dry mass. Energy density was calculated using 38 kJ/g for fat and 20 kJ/g for lean dry tissue (Ricklefs 1974). To make the body composition data comparable between species, fresh mass was expressed as a fraction of adult mass (Weathers 1996).

Energy budget

Prefledging energy budgets were constructed on the basis of the average body mass growth curve for free-living chicks of each species in the Netherlands:

Black-tailed Godwit: $M = 273 \times \exp(-\exp(-0.085 \times (a - 11.0)))$;

Northern Lapwing: $M = 236 \times \exp(-\exp(0.054 \times (a - 20.5)))$,

where a = age in days (Beintema & Visser 1989a), by inserting the relevant species-specific metabolic parameters at each mass. Daily metabolised energy (ME, kJ/d) was expressed as the sum of basal metabolism (BMR, kJ/d), heat loss due to assimilation of nutrients and tissue synthesis (E_{syn}, kJ/d), costs of thermoregulation and activity ($E_{tr+act,}$ kJ/d), and energy deposited into new tissue (E_{tis}, kJ/d) (e.g. Drent *et al.* 1992):

$$ME = BMR + E_{syn} + E_{tr+act} + E_{tis}.$$

The first three components together constitute DEE as measured by the DLW method. BMR was not measured directly, but resting metabolic rate (RMR, kJ/d) of recently-fed chicks in the thermoneutral zone was determined in the laboratory-raised chicks (Visser & Ricklefs 1993a,b). These measurements include both BMR and E_{syn}, and BMR was estimated by subtracting E_{syn} from RMR. E_{syn} was estimated as $0.78 \times E_{tis}$, based on the measured body composition and synthesis efficiencies for fat and protein in birds given by Blaxter (1989). E_{tis} was calculated as the daily increment of the product of body mass and energy density.

The remaining part of DEE represents the energy allocated to thermoregulation and activity. We refrained from making separate estimates for these components (e.g. Klaassen 1994), because the distinction between them is obscured by interaction effects. Physical disturbance of the insulative layer during locomotion and the contact with wet vegetation are likely to elevate a foraging chick's heat loss above resting levels. This elevation can be considered part of activity as much as of thermoregulation costs. In addition, (partial) substitution of thermoregulation costs by heat generated during activity is likely to occur (Webster & Weathers 1990, Bruinzeel & Piersma 1998).

Statistics

Power curves for energy expenditure or water turnover as a function of body mass were fitted as linear regressions on log-transformed data. Additional explanatory variables entered (temperature, growth rate) were not log-transformed, as this would have produced impossible predictions at values ≤0. Because repeated measurements on the same chick and on chicks from the same brood (or cage) do not constitute fully independent observations, variance component models were applied (Byrk & Raudenbusch 1992), that take into account that the data comprise several hierarchically nested error levels. For the field measurements, factors 'chick' and 'brood' were treated as random effects, and for the laboratory trials, 'cage'. Mass, growth rate and weather variables were treated as fixed effects. The program MLwiN (Rasbash *et al.* 1998) was used for model fitting. Differences between godwits and lapwings in these relationships were tested by including the factor 'species' (test for intercept) and the interaction between species and mass (test for slope) as fixed effects in models for the combined data. Significance of explanatory variables was evaluated by likelihood ratio tests using the difference in deviance between models including and excluding the variables of interest. All tests were two-tailed, and a value of $P = 0.05$ was used to accept significance. Means are presented ± 1 standard deviation unless indicated otherwise.

RESULTS

Carcass analysis

Because the sample of chick carcasses was small and covariance analysis did not show significant differences between species or between wild and captive chicks, we calculated common linear regressions of energy density (ED) and water content (%H_2O) on the fraction of adult mass attained (M_{ad}: Northern Lapwing 202 g, Black-tailed Godwit 273 g, mean values for both sexes in periods when no substantial fat stores are carried). Energy density was related to the fraction of adult mass attained as:

$ED = 4.38 + 3.21 \times M/M_{ad}$ (R^2=0.80, $F_{1,6}$=23.7, P=0.003),

increasing from 4.7 kJ/g^{-} at hatching to 7.6 kJ/g^{-} at adult mass (fig. 2.1a). Changes in energy density were primarily caused by changes in water content (fig. 2.1b), which decreased from 79% of fresh mass in hatchlings to 70% at adult mass:

$\%H_2O = 79.86 - 9.55 \times M/M_{ad}$ ($R^2=0.59$, $F_{1,6}=8.48$, $P=0.027$).

There was no significant relation between the fat content of carcasses and their relative mass ($F_{1,6}=0.14$, $P=0.72$), even when excluding the smallest chick with a high fat content that was probably due to residual yolk reserves ($F_{1,6}=1.47$, $P=0.28$; fig. 2.1c). Disregarding this individual, the mean fat content of shorebird chicks was 7.8 ± 4.5% of total dry mass. Using this proportion and synthesis efficiencies for fat and protein in birds (Blaxter 1989), synthesis costs were estimated as:

$E_{syn} = 0.78 \times E_{tis}$ (*cf.* Weathers 1996).

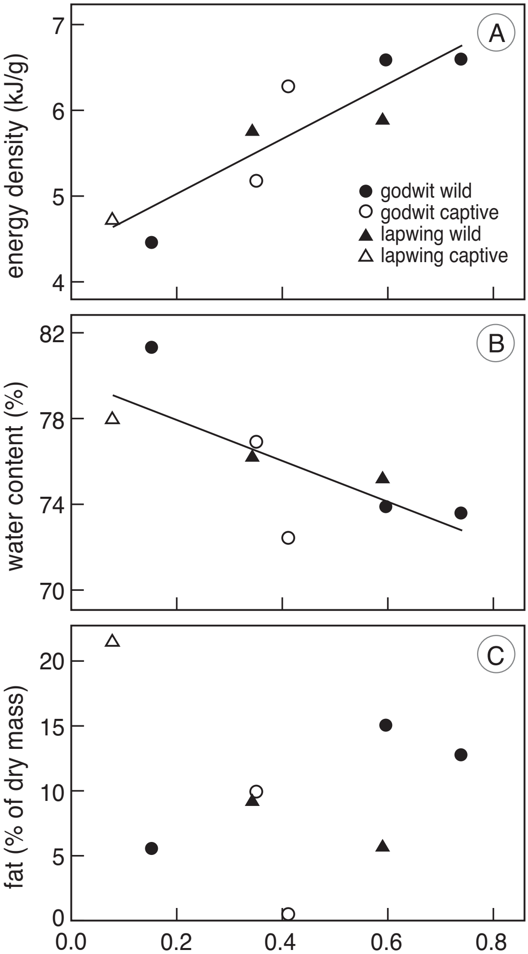


FIGURE 2.1. Body composition of chicks in relation to the fraction of adult mass attained. A: energy density; B: water content; C: fat as % of dry mass. Symbols refer to different categories of birds. Statistics in text.

Energy expenditure in the field

In total, 17 doubly labelled water (DLW) measurements were made on 13 Black-tailed Godwit chicks in 8 broods; 22 measurements were made on 16 NorthernLapwing chicks in 10 broods. A maximum of three measurements was made on a single chick, at intervals of at least four days. During measurements, godwit chicks grew between -4 and 14 g/d (mean 6.2 ± 4.7 g/d), which is on average 83 ± 68% (range -50 to 185 %) of the mean growth rate of free-living chicks in the Netherlands at the given body mass (Beintema & Visser 1989a). This value is not significantly different from 100% (t_{16}=1.00, P=0.16). Lapwing chicks grew between 0 and 12.3 g/d (mean 5.0 ± 3.2 g/d), on average 123 ± 82% (range 0 to 300%) of the mean growth rate of free-living chicks at the same mass, and again not significantly different from 100% (t_{21}=1.01, P=0.16). We conclude that the DLW dataset was representative with respect to the growth rate of chicks.

For Black-tailed Godwits, the relationship between daily energy expenditure (DEE, kJ/d) and body mass (M, g), fitted using a variance component model, was: DEE = 1.549 × $M^{1.092}$ (fig. 2.2a; statistics in table 2.1). For Northern Lapwings it was: DEE = 2.037 × $M^{1.047}$ (table 2.1). In neither species did the mass exponent differ significantly from unity (godwit, t_{16}=0.90, P=0.19; lapwing, t_{21}=0.68, P=0.25); hence relationships were

TABLE 2.1. Regression equations for daily energy expenditure (DEE, kJ/d), metabolised energy (ME, kJ/d) and water influx (H_2O_{in}, g/d) in free-living, and daily metabolised energy intake (MEI, kJ/d) in laboratory-raised chicks of Black-tailed Godwit and Northern Lapwing. Predictor variables used are mass (g), operative temperature (°C), and growth rate (g/d). LRT denotes likelihood ratio test for last-included variable (d.f.=1), i.e. for mass in models where only mass is included, and for the '2nd predictor' in other models.

response variable	predictor variable	regression coefficients ± SE			LRT	
		constant	log mass	2nd predictor	χ^2	P
Black-tailed Godwit						
log DEE	log mass	0.190 ± 0.205	1.092 ± 0.102	-	33.0	< 0.001
	+ temperature	0.173 ± 0.191	1.263 ± 0.106	−0.022 ± 0.007	5.74	0.017
log ME	log mass	0.552 ± 0.184	0.940 ± 0.090	-	29.5	< 0.001
	+ growth rate	0.330 ± 0.206	1.013 ± 0.103	0.014 ± 0.006	4.17	0.041
log H_2O_{in}	log mass	−0.668 ± 0.234	1.290 ± 0.119	-	35.9	< 0.001
log MEI	log mass	0.731 ± 0.121	0.824 ± 0.059	-	67.5	< 0.001
	+ growth rate	0.620 ± 0.059	0.806 ± 0.028	0.016 ± 0.002	54.9	< 0.001
Northern Lapwing						
log DEE	log mass	0.309 ± 0.128	1.047 ± 0.069	-	49.6	< 0.001
log ME	log mass	0.640 ± 0.137	0.911 ± 0.074	-	43.4	< 0.001
	+ growth rate	0.548 ± 0.109	0.0911 ± 0.057	0.018 ± 0.005	11.1	< 0.001
log H_2O_{in}	log mass	−0.663 ± 0.173	1.319 ± 0.092	-	45.1	< 0.001
log MEI	log mass	0.537 ± 0.060	0.884 ± 0.032	-	227.2	< 0.001
	+ growth rate	0.496 ± 0.048	0.858 ± 0.026	0.018 ± 0.002	53.1	< 0.001

essentially linear. Neither the intercepts (χ^2_1=1.09, P=0.30) nor the slopes (χ^2_2=1.33, P=0.52) of the relationships between DEE and mass differed significantly between species. Nevertheless, we used the species-specific equations for constructing energy budgets.

Metabolised energy (ME, kJ/d) was calculated by adding energy deposited in tissues (E_{tis}) to DEE if the animal gained weight during the DLW measurement, and set equal to DEE if no weight gain occurred. In Black-tailed Godwits, ME and body mass were related as ME = 3.565 × $M^{0.940}$; in Northern Lapwings as ME = 4.365 × $M^{0.911}$ (table 2.2; fig. 2.2b). In neither species did the mass exponent differ significantly from 1 (godwit, t_{16}=0.67, P=0.26; lapwing, t_{21}=1.20, P=0.12). Neither the intercepts (χ^2_2=1.16, P=0.28) nor the slopes (X^2_2=1.68, P=0.43) differed significantly between the species.

After allowing for the effect of body mass, the remaining variation in DEE was unrelated to growth rate in both species (Black-tailed Godwit χ^2_1=0.79, P=0.37, Northern Lapwing χ^2_1=1.91, P=0.17). However, the residual variation in ME after allowing for body mass was positively related to growth rate in both species (table 2.1), due to increasing amounts of energy deposited into tissue.

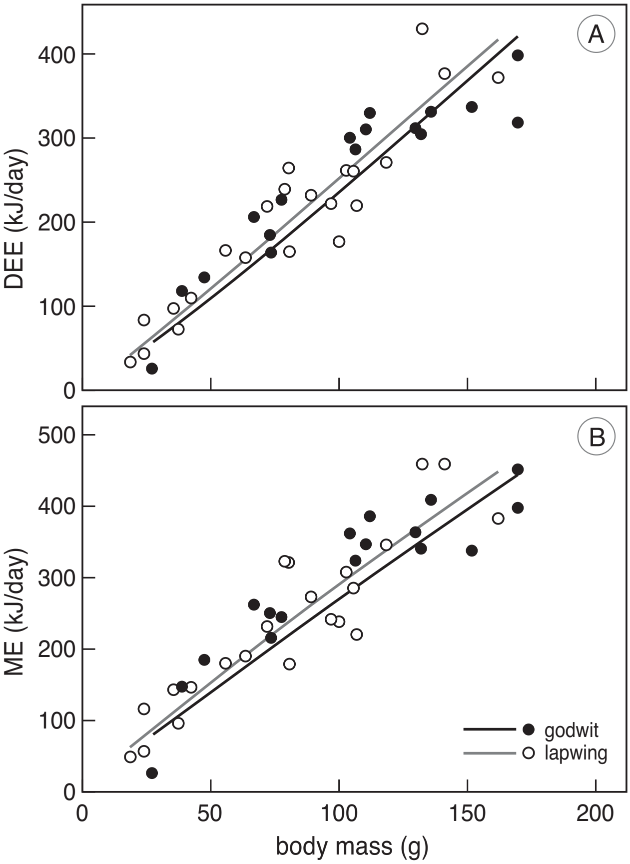


FIGURE 2.2. Daily Energy Expenditure (A) and daily Metabolised Energy (B) in chicks of Black-tailed Godwit and Northern Lapwing in relation to body mass. Lines represent the fitted allometric relationships (equations in table 2.1).

TABLE 2.2. Comparison of estimated total metabolised energy (TME) and energy expended on thermoregulation and activity (E_{tr+act}) of godwit and lapwing chicks growing up at identical growth rates in the field and in the laboratory.

species	energetic parameter	field (kJ)	laboratory (kJ)	savings in laboratory field-lab (kJ)	savings in laboratory (field-lab)/field (%)
Black-tailed Godwit	TME	8331	6166	2165	25.9
	E_{tr+act}	4124	1959	2165	52.5
Northern Lapwing	TME	6982	4832	2150	30.8
	E_{tr+act}	3688	1538	2150	58.3

Mean operative temperature (T_e) during the 39 DLW measurements was 15.7 ± 4.1°C (range 7.1-23.5°C), close to the average T_e of 15°C measured over the period when chicks were present. Mean wind speed was 4.3 ± 1.1 m/s (range 2.3-8.4 m/s). These figures were not different between measurements on Black-tailed Godwits and Northern Lapwings (t_{37}=0.37, P=0.72, resp. t_{37}=1.43, P=0.16). Rain fell during (part of) 19 out of 39 measurement periods. In godwits, DEE decreased with operative temperature after allowing for the effect of mass (table 2.1). The occurrence of rainfall also affected DEE (χ^2_1=3.95, P=0.047), but the effect of wind speed was not significant (χ^2_1=2.46, P=0.12). In lapwings, effects of operative temperature (χ^2_1=0.0, P=1.0), wind speed (χ^2_1=3.64, P=0.06), and rainfall (χ^2_1=0.07, P=0.79) were not significant. Weather variables did not explain residual variation after allowing for the effect of mass on ME in either species (all P>0.12).

Water flux

Daily water influx of Black-tailed Godwit chicks (H_20_{in}, g/d) was related to body mass as: $H_20_{in} = 0.215 \times M^{1.290}$, of Northern Lapwing chicks as $H_20_{in} = 0.217 \times M^{1.319}$ (table 2.1). Intercepts (χ^2_2=1.60, P=0.21) and slopes (χ^2_2=2.25, P=0.32) were not significantly different for the two species. Water influx rates in chicks were markedly higher than predicted from a mass-based allometric relationship for adult wild birds in the field (Nagy & Peterson 1988): the mean difference was +146 ± 72% (N=17) for godwits, and +141 ± 87% (N= 22) for lapwings.

Field energy budgets

Total energy requirements of Northern Lapwings and Black-tailed Godwits increased throughout the prefledging period, without a maximum or plateau before fledging as found in several altricial and semiprecocial birds (fig. 2.3). ME reached the highest value (godwit, 556 kJ/d, lapwing 399 kJ/d) at fledging, but probably still further increases thereafter because the chicks continue growing for some time (Beintema & Visser 1989a). Taking the age of fledging (25 days for godwits, 33 days for lapwings; H. Schekkerman unpubl.) as a natural endpoint for interspecific comparisons, the total metabolised energy over this period (TME) amounted to 8331 kJ in godwits and 6982 kJ in lapwings. Average Daily Metabolised Energy (ADME), which is TME divided by both fledging mass (godwit 201 g, lapwing 142 g) and the time to fledging (Weathers 1992), was 1.66 kJ/g/d in godwits and 1.49 kJ/g/d in lapwings.

The allocation of energy to different components of the budget was very similar in the two species (fig. 2.3). The proportion of TME made up by E_{tis} was estimated at 15% in Black-tailed Godwits and 13% in Northern Lapwings. Resting metabolism amounted to 35% of the total energy requirements in both species, of which about 24% was estimated to be basal metabolism and 11% synthesis costs. The remaining part of TME (50 and 53%) was spent on thermoregulation and activity.

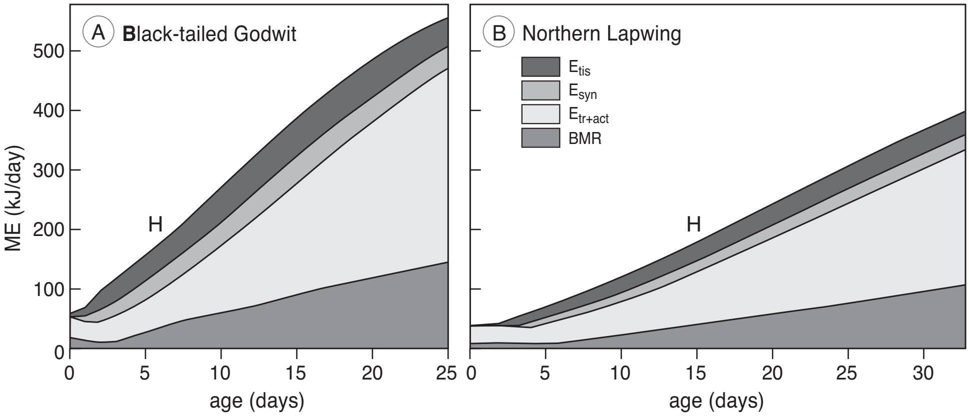
Energy expenditure in the laboratory

Captive Northern Lapwing chicks achieved a mean growth rate of 4.9 ± 2.3 g/d (range 0.3-11.3, N=114) during food intake trials, similar to the birds in the DLW sample and slightly higher than the average for Dutch chicks in the field. In contrast, the lab-raised Black-tailed Godwits grew on average 8.7 ± 4.1 g/d (range 2-19.7 N=48), which is 40% more than chicks subjected to DLW measurements in the field and also more than the average free-living chick.

Metabolisable energy intake (MEI, kJ/d) of laboratory-raised Black-tailed Godwit chicks was related to body mass as: $MEI = 5.382 \times M^{0.824}$; in Northern Lapwings this relationship was: $MEI = 3.444 \times M^{0.884}$ (table 2.1). In both species, growth rate explained a significant part of the residual variation in MEI after including body mass (table 2.1).

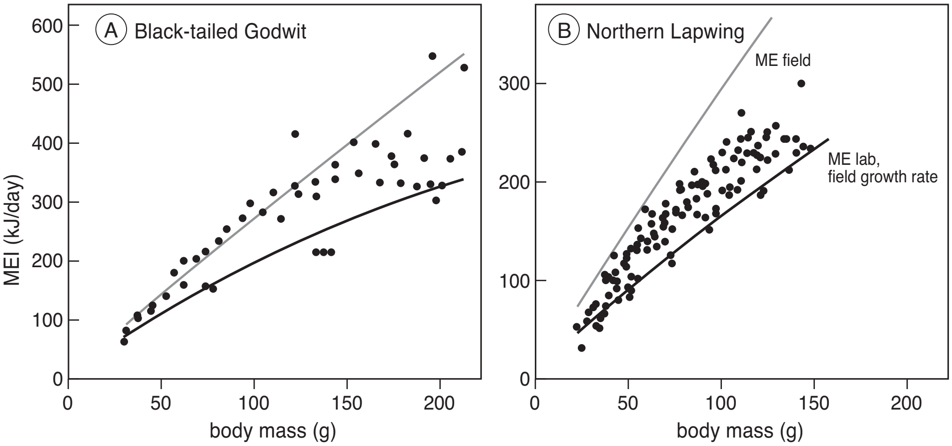
MEI of captive Black-tailed Godwits was similar to ME found in the field up to *c.* 100 g, but fell behind at higher body masses. In Northern Lapwing chicks, it was markedly lower in the laboratory than in the field at all masses (fig. 2.4). In view of the differences in growth rate between laboratory and field chicks, energy budgets for these groups were made comparable by inserting the average growth of free-living

FIGURE 2.3. Prefledging energy budgets for free-living Black-tailed Godwits and Northern Lapwings growing at the average rate, from hatching to fledging. Components shown are basal metabolic rate (BMR), cost of biochemical synthesis (E_{syn}), activity and thermoregulation (E_{tr+act}), and energy deposited into new tissue (E_{tis}). 'H' denotes the age at which homeothermy is achieved at 10°C (from Visser & Ricklefs 1993b).



chicks into the equation relating MEI to mass and growth rate (see table 2.1). The resulting estimates of total MEI over the prefledging period were 26% and 31% lower in godwits and lapwings respectively, than TME values obtained with DLW in the field. Because at the same growth rate BMR, E_{syn} and E_{tis} can be assumed equal in the field and in captivity, the difference must be due to thermoregulation and activity costs. Estimated total E_{tr+act} up to fledging was 53% and 58% lower in the laboratory than in the field for lapwings and godwits respectively (table 2.2).

FIGURE 2.4. Metabolisable Energy Intake (MEI, dots) of laboratory-raised chicks of Black-tailed Godwit (A) and Northern Lapwing (B) in relation to body mass. Continuous lines indicate the expected metabolised energy (ME) of chicks in the field (thin) and the expected MEI of laboratory chicks growing at the same rate as chicks in the field (thick).



DISCUSSION

General

To our knowledge, this study is the first to measure energy metabolism of self-feeding precocial chicks in the field. Below, we compare these estimates with data for other bird species, as a first test of the idea that the active and exposed lifestyle of self-feeding precocials leads to high energy requirements. This idea also predicts that the proportion of total metabolised energy (TME) allocated to thermoregulation and activity (E_{tr+act}) is relatively large in this group. We also discuss that E_{tr+act} is likely to be underestimated in captivity, so that it is important to make comparisons based on data obtained in the field. The fact that field measurements in godwits were made in enclosures did not affect their energy budgets in such a way that growth rates during DLW trials significantly differed from those of free-living chicks. All measurements in Northern Lapwings were made on free-living chicks.

Weathers (1992) discussed the accuracy of estimates of prefledging energy requirements, which consist of several separately estimated components. He concluded that estimates based on respirometry or food consumption experiments may involve errors of ±25%, but that errors in studies using doubly labelled water (DLW) are smaller, usually less than ±8%. Schekkerman and Visser (1999) found an average discrepancy of ±8.1% between simultaneous measurements obtained using DLW and respiration gas analysis in captive godwit and lapwing chicks. Since daily energy expenditure (DEE), as measured with DLW, makes up 85-87% of TME in chicks in the field, estimation of energy deposited into tissues (E_{tis}, error *c.* 5%) contributes little to errors in TME, which therefore will be also close to ±8%. Because the coefficients of variation for the estimates of gross energy content of the food (0.1%,) and for the digestive efficiencies (3.7% and 3.1% for Black-tailed Godwit and Northern Lapwing respectively, see materials and methods) are low, the average random error in the MEI estimates for the lab-raised chicks will probably be lower than 5%.

Body composition of precocial young

Precocial and semiprecocial birds hatch with greater locomotory and thermoregulatory abilities than altricials, reflected in functionally more mature tissues with lower water content (Ricklefs 1983, Starck & Ricklefs 1998). As water content and energy density (ED) of tissue are inversely related, precocials and semiprecocials should show higher ED at hatching than altricials (Ricklefs 1974). In line with this, the intercepts of regression equations relating ED to fraction of adult mass for six semiprecocial birds (mean 4.03 ± 0.23) listed in a review by Weathers (1996) are significantly higher than for the 10 altricials (2.92 ± 0.45, t_{14}=5.55, P<0.001). The only precocial included, the Japanese Quail *Coturnix coturnix*, showed the highest intercept (4.39), similar to the value for shorebird chicks (4.38).

Because adult body composition is not affected by developmental mode, a high intercept should lead to a shallower slope in (semi)precocial young (Ricklefs 1974). This difference is not significant in Weathers' (1996) dataset however, (altricials 5.03 ± 0.96, semiprecocials 4.67 ± 0.51; t_{14}=0.84, P=0.41), perhaps because of the deposition of prefledging fat stores in the semiprecocial seabirds included. The shorebird chicks did not lay down such stores, and the large intercept and shallow slope found in the carcass analysis thus conform to expectation.

Differences between lapwings and godwits

Despite the fact that fledging mass of Northern Lapwings was 29% lower than in Black-tailed Godwits, total metabolised energy (TME) over the prefledging period was only 16 % lower. This was due to the fact that young lapwings fledge at a 32% older age than godwits, causing the costs of basal metabolism, thermoregulation and activity to accrue over a longer period.

Slow growth has been interpreted as a mechanism to reduce daily energy requirements, thus alleviating the daily work load of the parents (e.g. Lack 1968, Drent & Daan 1980) or, in self-feeding precocials, the chicks. Beside a direct saving through the reduction of tissue formation, there may be an additional saving if basal metabolism is coupled to growth rate, as hypothesised by Drent & Klaassen (1989) and Klaasen

& Drent (1991). Indeed, over much of the prefledging period, mass-specific resting metabolic rate (RMR) in the thermoneutral zone is lower in young Northern Lapwings than in chicks of both the larger Black-tailed Godwit and the smaller Ruff *Philomachus pugnax* and Redshank *Tringa totanus* (Visser & Ricklefs 1993a). These three species belong to the Scolopacidae (snipes, sandpipers and allies), which grow faster than plovers and lapwings (Charadriidae; Beintema & Visser 1989a). It has been suggested that the slower growth of plovers may be related to an evolutionary past in semi-arid regions, warmer but generally poorer in food than the boreal marshes and arctic tundra where most Scolopacidae occur. This would make a reduction of metabolism and growth rate both climatically permissible and energetically advantageous (Beintema & Visser 1989b). In contrast, the high-latitude provenance of sandpipers, through a short season suitable for reproduction, may have selected for rapid growth (Chapter 3, Carey 1986) at the expense of higher energy requirements.

Despite the differences in growth rate and RMR, mass-specific daily energy expenditure and metabolised energy did not differ significantly between free-living Northern Lapwings and Black-tailed Godwits, and average daily metabolised energy (ADME) differed by only 10%. Either, the lapwings' savings on growth and resting metabolism were obscured by sampling variation, or they were offset by increased expenditure on other components of the budget. Because minimal thermal conductance does not differ between lapwings and godwits at the same mass (Visser & Ricklefs 1993b), this could be due to differences in the thermal environment (e.g. amount of shelter) or foraging activity. Because we estimated thermoregulation and activity costs jointly and by subtraction of the other budget components from ME, we are unable to unravel this further.

Energetic costs of self-feeding precociality

Weathers (1992) reviewed data on prefledging energy requirements for 30 bird species (20 (semi)altricials, 8 semiprecocials and 2 precocials, mostly from the temperate zone), and found that total energy metabolised over the fledging period increases with both body mass and age at fledging, the average deviation of observed from predicted values being only ±14%. TME of Black-tailed Godwits (8331 kJ) and Northern Lapwings (6982 kJ) was 39% and 29% higher than predicted by this relationship (6004 and 5422 kJ respectively). This difference is larger than the potential error in TME estimates (*c.* 8-25%, Weathers 1992). Estimates of average daily metabolised energy per gram of fledgling produced (ADME, 1.66 and 1.49 kJ/g/d for godwits and lapwings respectively) were 54% and 27% above Weathers' (1992) predictions (1.08 and 1.17 kJ/g/d). The value for godwits differed more from the prediction than those for any of the 30 species listed. Finally, the highest values of ME found before fledging (peak DME, 556 and 399 kJ/d) were 53% and 69% above allometric predictions (364 and 236 kJ/d, Weathers 1992). Fledging age of lapwings and godwits is within the range found in similar-sized species in Weathers's sample, so these comparisons do not involve extrapolations.

Hence, Black-tailed Godwit and Northern Lapwing chicks show high energy requirements compared to other birds for which data are available. This is probably due to their self-feeding lifestyle, involving much locomotor activity and high thermoregulation costs because of the need to forage outside the shelter of a nest. If so, high energy requirements should be a general characteristic of self-feeding precocial chicks, especially in temperate and cold climates, and the activity-thermoregulation component of the energy budget should be large in this group compared to parent-fed birds. Estimates of TME in captive self-feeding young ducks and quails (Sugden & Harris 1972; Cain 1976, Blem 1978, Blem & Zara 1980) are between 18% lower and 5% higher than the allometric predictions, but these studies are likely to have underestimated field metabolism as food was available *ad libitum* and holding facilities were generally heated and sometimes restricted locomotor activity (see below). Norton's (1973) estimate of TME in Dunlins *Calidris alpina* raised indoors is only 1% above the allometric prediction, but he estimated that free-living chicks in the Alaskan tundra would require 40% (Norton 1970) to 100% (Norton 1973) more energy. Field measurements using DLW in another arctic shorebird, the Red Knot *Calidris canutus*, revealed a TME that was 89% above the predicted value (Schekkerman et al. 2003, Chapter 3). These high values probably reflect the interaction of precociality with the cold arctic environment.

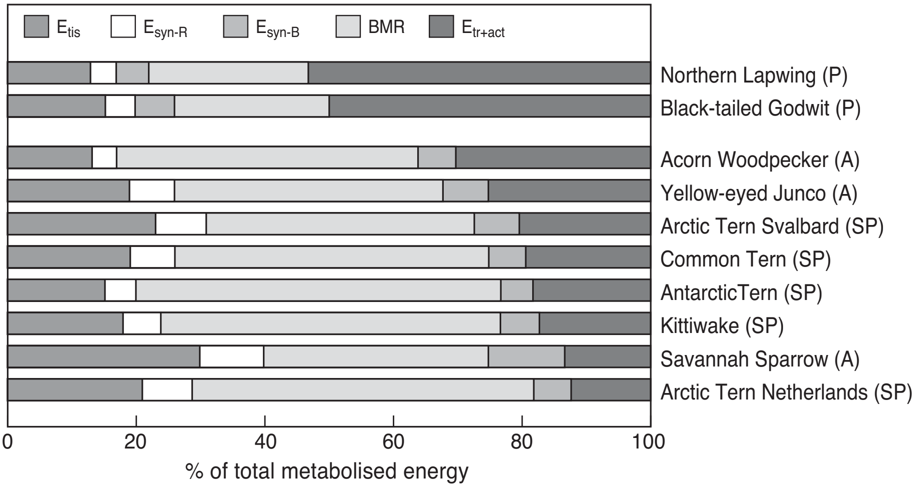
In Black-tailed Godwits and Northern Lapwings, 50-53% of TME was allocated to thermoregulation and activity (E_{tr+act}). These proportions can be compared to those in three altricial and four semiprecocial species for which DLW-based field energy budgets are available (fig. 2.5). All these studies assumed a synthesis efficiency of 75% (Ricklefs 1974), a value that is considered too high by some workers (e.g. Weathers 1996, but see Konarzewski 1995, Ricklefs *et al.* 1998). Because E_{tr+act} is found by subtracting BMR and synthesis costs (E_{syn}) from DEE, underestimation of E_{syn} leads to overestimation of E_{tr+act}. Recalculation of E_{tr+act} for the seven parent-fed species, using efficiency estimates following Blaxter (1989), results in proportions of TME averaging 19 ± 6% (range 12-30%, N=8). Uncorrected values averaged 26 ± 6% (range 18-36%), still only half the value found in shorebirds.

The high thermoregulation and activity costs in shorebird chicks agree with observations on their time-activity budgets. Black-tailed Godwit chicks in the field spend 7-16 hours per day (50-90%, average 80%, of the 16 h daylight period in chicks older than a week) actively searching for prey, walking distances of 4-10 km/d (Chapter 5). Northern Lapwing chicks receive more parental brooding than godwits (Beintema and Visser 1989b), but chicks ≥7 days old spend *c.* 70% of the daylight period actively foraging. In contrast, chicks of the semiprecocial Common Tern *Sterna hirundo* and Arctic Tern *S. paradisaea*, even when hardly brooded anymore at ages ≥15 days, allocate less than 20% of the daylight period to activity (Klaassen *et al.* 1994). Altricial House Wren *Troglodytes aedon* nestlings 6-10 days old spend even less time on active behaviours (shivering, small movements, and begging): 4-8% of the 14 h day (Bachman & Chappell 1998).

Energy requirements in laboratory and field

If thermoregulation and foraging cause the high energy expenditure in free-living shorebird chicks, it can be expected that metabolism is reduced in the laboratory, where chicks are not exposed to cold and wind and food is available without effort. The scope for saving energy in captivity would be larger in self-feeding precocials than in altricials and semiprecocials with lower natural activity levels. In line with this, ME of the laboratory-raised shorebirds was generally lower than that of free-

FIGURE 2.5. Prefledging energy budgets for Black-tailed Godwit and Northern Lapwing in the field and in the laboratory (this study), compared with DLW-based field budgets for Acorn Woodpecker *Melanerpes formicivorus* (Weathers *et al.* 1990), Yellow-eyed Junco *Junco phaeonotus* (Weathers & Sullivan 1991), Arctic Tern *Sterna paradisaea* (Spitsbergen, Klaassen *et al.* 1989; Netherlands, Klaassen 1994), Common Tern *S. hirundo* and Antarctic Tern *S. vittata* (Klaassen 1994), Kittiwake *Rissa tridactyla* (Gabrielsen *et al.* 1992) and Savannah Sparrow *Passerculus sandwichensis* (Williams & Prints 1986). Acronyms denote ontogenic types: P precocial, SP semiprecocial, A altricial. Species are ordered according to the proportion of total metabolism allocated to thermoregulation and activity (E_{tr+act}). E_{syn-B} denotes the increase in the estimate of synthesis costs above that based on a synthesis efficiency of 75 % (E_{syn-R}) caused by using synthesis efficiencies from Blaxter (1989). In the shorebird budgets this difference led to a lower estimate of BMR; in the other species to a lower estimate of E_{tr+act}.



ranging chicks at the same mass. After correcting for growth rate differences, E_{tr+act} was estimated 53-58% lower in the lab than in the field, resulting in a 26-31% lower TME (table 2.2). Nevertheless, the savings in captive shorebirds were not much larger than the 25% difference between field and laboratory ME reported for altricial Savannah Sparrows *Passerculus sandwichensis* by Williams & Prints (1986). Their measurements of oxygen consumption in small metabolic chambers at thermoneutrality probably included negligible E_{tr+act}, while this component was still substantial during our food intake trials. Had E_{tr+act} been negligible in the captive shorebird chicks, the difference with field metabolism would have been 50-53%. We conclude that laboratory measurements are likely to substantially underestimate energy requirements especially in self-feeding precocial chicks.

Ecological implications of self-feeding precociality

Compared to parent-fed nestlings of similar size, young shorebirds need to ingest more food to sustain themselves. In addition, their lifestyle does not provide much leeway in periods of food scarcity. Because foraging is by far the most important form of activity, shorebird chicks cannot save energy by reducing activity, as observed in semiprecocial terns (Klaassen *et al*. 1994), without further reducing food intake. Only if feeding intake rate falls below the concomitant energy expenditure should chicks stop foraging. They might save some energy by selecting sheltered microhabitats (Wiersma & Piersma 1994), but the potential savings are probably small. Even in good conditions, Black-tailed Godwits forage mostly in tall grass, where wind influence is much reduced (Klaassen 1994); variation in wind speed at 3 m height had no discernible effect on DEE in godwits. Hence, they can hardly find more shelter when conditions deteriorate. In addition, reduced food availability for young of both species is often associated with windy and cold or wet weather (Chapter 5), and will thus tend to coincide with increased thermoregulation costs due to low temperature or rain, which may offset any savings due to wind shelter. Chicks may also compensate for a reduced foraging yield by increasing foraging time, but since they already spend most (*c*. 80%) of the daylight period foraging under normal conditions, scope for this is limited, and it is further reduced when chicks need to be brooded more often during cold weather (Beintema & Visser 1989b, Chapter 5).

If basal metabolism, activity, and thermoregulation cannot be substantially economised upon, it is inevitable that energy shortage soon results in reductions in growth rate. The proportion of TME that is allocated to growth (E_{tis}+E_{syn}) is comparatively small in the shorebirds: 23-27%, compared to 24-52% (mean 33%), in the seven altricials and semiprecocials in fig. 2.5 (note that under the alternative assumption of 75% synthesis efficiency, the proportion of TME allocated to growth is only 17-20% in the shorebirds). This implies that small reductions in energy intake may lead to stagnation of growth. Our data further show that shorebird chicks do not carry substantial fat deposits that enable them to overcome long periods of food scarcity: a two-week old, 126 g godwit chick carries *c*. 10 g of fat, which is enough to sustain its normal DEE for 1.3 days. These points suggest that self-feeding shorebird chicks operate within fairly narrow energetic margins, and therefore depend on a reliable food supply for successful development.

On the other side of the coin, parents of self-feeding precocials do not have to spend time and energy procuring and transporting food to their young. Although field measurements of energy expenditure in parent birds tending self-feeding chicks are still too scarce to reveal patterns, it seems likely that they will be lower than those of birds that do feed their young, if only because costly flights with food are unnecessary. In addition, precocial parents may be less time-limited, because feeding for their own needs is more compatible with guarding a brood than with collecting food for them. Thus, the parents are partially relieved from one of the most energetically stressful periods in the annual cycle (Drent & Daan 1980, Tatner & Bryant 1993), and this may enhance their survival or future fecundity (Daan *et al*. 1996, Golet *et al*. 1998).

From a chick's viewpoint, the need to transport food is costly too, because the profitability of prey is reduced by the time lost on transportation. The extent of this reduction decreases with the energetic yield of the load (and increases with transportation distance). Hence, unless multiple-prey loading is possible, transporting food to the young is especially unprofitable, shifting the evolutionary balance towards self-feeding, when the prey are of low energetic value, or small relative to body size. At the same time, capturing large and energy-rich prey may often require strength and skills not present in small young (Nice 1962; Ricklefs & Starck 1998). These points may explain why self-feeding is common in young of herbivorous birds (geese, some gamebirds; low-energy food) and among medium-sized species which feed on invertebrates that occur in high densities but are of small size (ducks, shorebirds, and gamebirds). A further energetic advantage of self-feeding for chicks is that scramble competition for food between brood mates can be largely avoided, although interference competition may still occur.

Conclusion

The limited data available to date suggest that a high energy expenditure on activity and thermoregulation associated with foraging in self-feeding shorebird chicks makes this mode of development energetically costly. Field measurements on shorebirds which are fed by their parents (oystercatchers, stone-curlews, snipes), and on species in other self-feeding precocial taxa like Anseriforms and Galliforms, are needed to confirm that this pattern is unique to, and general among, birds with self-feeding young. Such measurements will also provide an empirical basis for models for exploring the relative performance of self-feeding and parental feeding under different conditions of climate and food availability, which may shed some light on the evolution of avian developmental modes. In such models, it is important to consider the family unit as a whole, which means that measurements of energy expenditure in parent birds tending self-feeding young are also called for.

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REFERENCES

- Bachman G.C. & M.A. Chappell 1998. The energetic cost of begging behaviour in nestling house wrens. Animal Behavior 55: 1607-1618.
- Bakken G.S., W.R. Santee & D.J. Erskine 1985. Operative and standard operative temperature: tools for thermal energetics studies. American Zoologist 25: 933-934.
- Beintema A.J. & G.H. Visser 1989a. Growth parameters in chicks of charadriiform birds. Ardea 77: 169-180.
- Beintema A.J. & G.H. Visser 1989b. The effect of weather on time budgets and development of meadow birds. Ardea 77:181-192.
- Beintema A.J., J.B. Thissen, D. Tensen & G.H. Visser 1991. Feeding ecology of charadriiform chicks in agricultural grassland. Ardea 79: 31-44.
- Blaxter K. 1989. Energy metabolism in animals and man. Cambridge University Press, Cambridge.
- Blem C.R. 1978. The energetics of young Japanese Quail, *Coturnix coturnix japonica*. Comparative Biochemical Physiology 59A: 219-223.
- Blem C.R & J. Zara 1980. The energetics of young Bobwhite *(Colinus virginianus)*. Comparative Biochemical Physiology 67A: 611-615.
- Bruinzeel L.W. & T. Piersma 1998. Cost reduction in the cold: heat generated by terrestrial locomotion partly substitutes for thermoregulation costs in Knot *Calidris canutus*. Ibis 140: 324-328.
- Byrk A.S., and S.W. Raudenbush 1992. Hierarchical linear models, application and data analysis. Sage, London.
- Cain B.W. 1976. Energetics of growth for Black-bellied Tree Ducks. Condor 78:124-128.
- Carey C. 1986. Avian reproduction in cold climates. In H. Ouellet (Ed.) Acta XIX Congressus Internationalis Ornithologici, Ottawa, Ontario, 1986: 2708-2715. National Museum of Natural Sciences, Ottawa.
- Daan S., C. Deerenberg & C. Dijkstra 1996. Increased daily work precipitates death in the Kestrel. Journal of Animal Ecology 65: 539-544.
- Drent R.H. & S. Daan 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.
- Drent R. & M. Klaassen 1989. Energetics of avian growth: the causal link with BMR and metabolic scope. In C. Bech & R.E. Reinertsen (eds), Physiology of cold adaptation in birds: 249-359 Plenum, New York.
- Drent R.H., M. Klaassen & B. Zwaan 1992. Predictive growth budgets in terns and gulls. Ardea 80: 5-17.
- Gabrielsen G.W., M. Klaassen & F. Mehlum 1992. Energetics of Black-legged Kittiwake *Rissa tridactyla* chicks. Ardea 80: 9-40.
- Gessaman A. & K.A. Nagy 1988. Energy metabolism: errors in gas-exchange conversion factors. Physiological Zoology 61: 07-513.
- Golet G.H., D.B. Irons & J.A. Estes 1998. Survival costs of chick rearing in black-legged kittiwakes. Journal of Animal Ecology 67: 827-841.
- Hagemeijer E.J.M. & M.J. Blair 1997. EBCC Atlas of European breeding birds. Poyser, London.
- Klaassen M. 1994. Growth and energetics of tern chicks from temperate and polar environments. Auk 111: 525-544.

- Klaassen M. & R.H. Drent 1991. An analysis of hatchling resting metabolism: in search of ecological correlates that explain deviations from allometric relations. Condor 93: 612-629.
- Klaassen M., C. Bech, D. Masman & G. Slagsvold 1989. Growth and energetics of Arctic Tern chicks (*Sterna paradisaea*). Auk 106: 240-248.
- Klaassen M. 1994. Growth and energetics of tern chicks from temperate and polar environments. Auk 111: 525-544.
- Klaassen M., B. Habekotté, P. Schinkelshoek, E. Stienen & P. van Tienen 1994. Influence of growth rate retardation on time budgets and energetics of Arctic Tern *Sterna paradisaea* and Common Tern *S. hirundo* chicks. Ibis 136: 197-204.
- Konarzewski M. 1995. Allocation of energy to growth and respiration in avian post-embryonic development. Ecology 76: 8-19.
- Lack D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Lifson N. & R. McClintock 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. Journal of Theoretical Biology 12: 46-74.
- Nagy K.A. 1980. CO_2-production in animals: analysis of potential errors in the doubly labelled water method. American Journal of Physiology 238: R466-R473.
- Nagy K.A. & S.C. Peterson 1988. Scaling of water flux rate in animals. University of California Publications in Zoology 120.
- Nice M.M. 1962. Development of behavior in precocial birds. Transactions of the Linnean Society, New York 8: 1-211.
- Norton D.W. 1970. Thermal regimes of nests and bioenergetics of chick growth in the Dunlin (*Calidris alpina*) at Barrow, Alaska. M.Sc. Thesis, University of Alaska, Fairbanks.
- Norton D.W. 1973. Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph.D. Dissertation, University of Alaska, Fairbanks.
- Rasbash J., M. Healy, W. Browne & B. Cameron 1998. MLwiN version 1.00. Multilevel Models Project, Institute of Education, University of London, London.
- Ricklefs R.E. 1973. Patterns of growth in birds II. Growth rate and mode of development. Ibis 115: 177-201.
- Ricklefs R.E. 1974. Energetics of reproduction in birds. In R.A. Paynter (ed.), Avian Energetics: 152-292. Publications of the Nutall Ornithological Club no. 15.
- Ricklefs R.E. 1983. Avian postnatal development. In D.S. Farner, J.R. King & K.C. Parkes (eds), Avian biology, Vol. 7: 1-83. Academic Press, New York.
- Ricklefs R.E. & J.M. Starck. 1998. The evolution of the developmental mode in birds. In J.M. Starck & R.E. Ricklefs (eds), Avian growth and development: 366-380. Oxford University Press, New York.
- Ricklefs R. E., J.M. Starck & M. Konarzewski 1998. Internal constraints on growth in birds. In J.M. Starck & R.E. Ricklefs (eds), Avian growth and development: 266-287. Oxford University Press, New York.
- Speakman J.R. 1997. Doubly labelled water. Theory and practice. Chapman & Hall, London.
- Sugden L. & L. E. Harris 1972. Energy requirements and growth of captive Lesser Scaup. Poultry Science 51: 625-633.
- Starck J.M. & R.E. Ricklefs 1998. Patterns of development: the altricial-precocial spectrum. In J.M. Starck & R.E. Ricklefs (eds), Avian growth and development: 3-30. Oxford University Press, New York.

- Tatner P. & D.M. Bryant 1993 Interspecific variation in daily energy expenditure during avian incubation. Journal of Zoology (London) 231: 215-232.
- Visser G.H., & R. E. Ricklefs 1993a. Temperature regulation in neonates of shorebirds. Auk 110: 445-457.
- Visser G.H. & R.E. Ricklefs 1993b. Development of temperature regulation in shorebirds. Physiological Zoology 66: 771-792.
- Visser G.H. & H. Schekkerman 1999. Validation of the doubly labelled water method in growing precocial birds: the importance of assumptions concerning evaporative water loss. Physiological & Biochemical Zoology 72:740-749.
- Walsberg G.E. & W.W. Weathers 1986. A simple technique for estimating operative environmental temperature. Journal of Thermal Biology 11: 67-72.
- Weathers W.W. 1992. Scaling nestling energy requirements. Ibis 134: 142-153.
- Weathers W.W. 1996. Energetics of postnatal growth. In C. Carey (ed.), Avian energetics and nutritional ecology: 461-496. Chapman & Hall, New York.
- Weathers W.W., W.D. Koenig & M.T. Stanback 1990. Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. Condor 92: 341-359.
- Weathers W.W. & K.A. Sullivan 1991. Growth and energetics of nestling Yellow-eyed Juncos. Condor 93: 138-146.
- Webster M.D. & W.W. Weathers 1990. Heat produced as a byproduct of foraging activity contributes to thermoregulation by Verdins *Auriparus flaviceps*. Physiological Zoology 63: 777-794.
- Wiersma P. & T. Piersma 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. Condor 96: 257-279.
- Williams J.B. & A. Prints 1986. Energetics of growth in nestling Savannah Sparrows: a comparison of doubly-labelled water and laboratory estimates. Condor 88: 74-43.

Mechanisms promoting higher growth rate in arctic than temperate shorebirds

3

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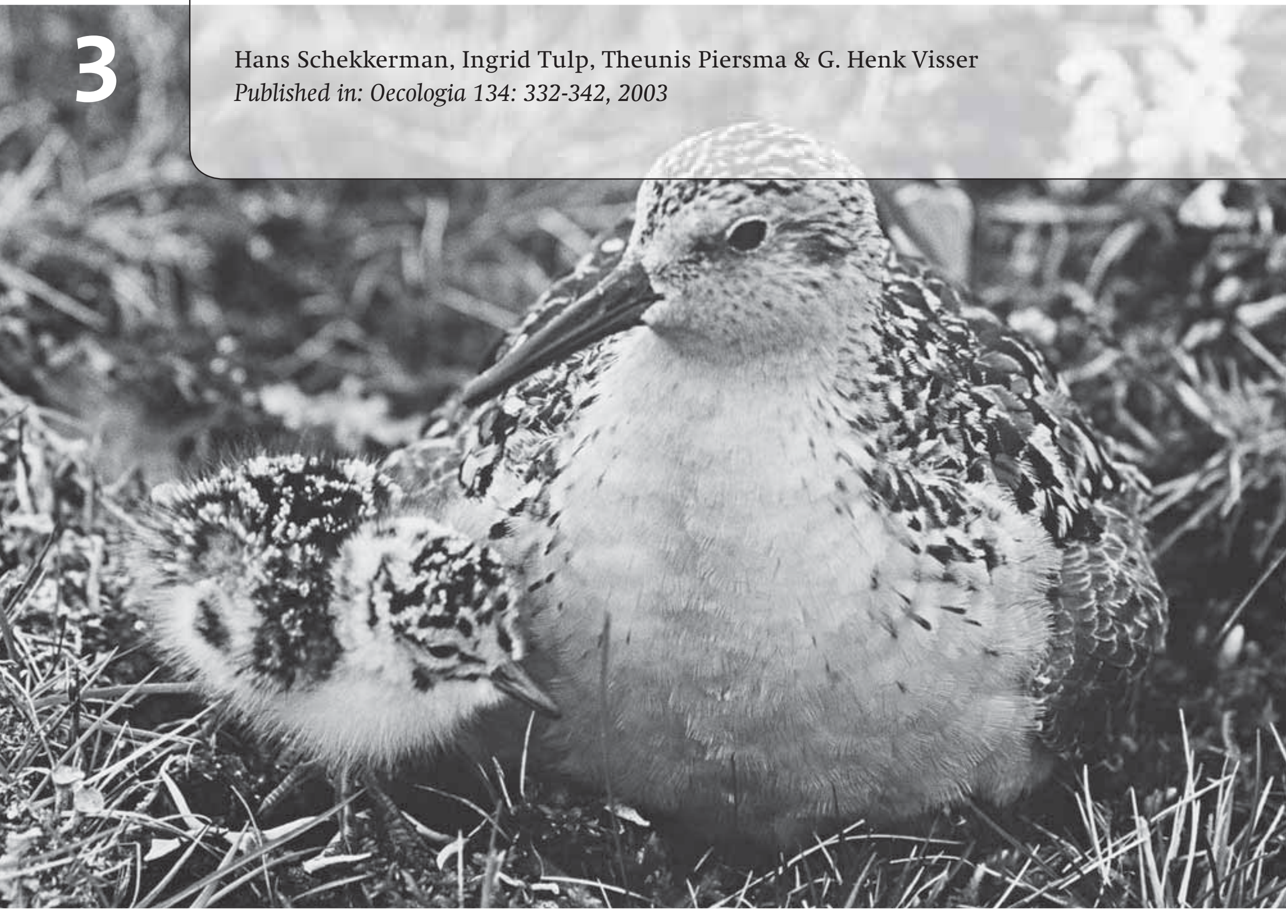


1. We compared prefledging growth, energy expenditure, and time budgets in the arctic-breeding Red Knot *Calidris canutus* to those in temperate shorebirds, to investigate how arctic chicks achieve a high growth rate despite energetic difficulties associated with precocial development in a cold climate.

2. Growth rate of knot chicks was very high compared to other, mainly temperate, shorebirds of similar size, but strongly correlated with weather-induced and seasonal variation in availability of invertebrate prey. Red Knot chicks sought less parental brooding and foraged more at the same mass and temperature than chicks of three temperate shorebird species studied in the Netherlands.

3. Fast growth and high muscular activity in the cold tundra environment led to high energy expenditure, as measured using doubly labelled water: total Metabolised Energy over the 18 day prefledging period was 89% above an allometric prediction, and among the highest values reported for birds.

4. A comparative simulation model based on our observations and data for temperate chicks showed that several factors combine to enable Red Knots to meet these high energy requirements: (1) the greater cold-hardiness of Red Knot chicks increases time available for foraging; (2) their fast growth further shortens the period in which chicks depend on brooding; (3) the 24-h daylight increases potential foraging time, though knots apparently did not make full use of this. These mechanisms buffer the loss of foraging time due to increased need for brooding at arctic temperatures, but not enough to satisfy the high energy requirements without invoking (4) a higher foraging intake rate as an explanation. Since surface-active arthropods were not more abundant in our arctic study site than in a temperate grassland, this may be due to easier detection or capture of prey in the tundra. The model also suggested that the cold-hardiness of Red Knot chicks is critical in allowing them sufficient feeding time during the first week of life.

5. Chicks hatched just after the peak of prey abundance in mid-July, but their food requirements were maximal at older ages, when arthropods were already declining. Snow cover early in the season prevented a better temporal match between chick energy requirements and food availability, and this may enforce selection for rapid growth.

INTRODUCTION

Compared to temperate and tropical environments, arctic regions present two main problems to warm-blooded animals: the cold climate imposes high thermoregulary costs, which must be matched by food intake, and a short period of increased food availability sets a narrow window for reproduction in many species (e.g. Chernov 1985, Carey 1986). The selective force thus exerted on arctic animals includes morphological, physiological and behavioural characteristics. With respect to reproduction, developmental mode and growth rate of offspring are traits likely to be affected by this selection, as they affect both time and amount of energy required.

Many species of shorebirds (Charadrii), especially within the Scolopacidae (sandpipers, snipes and allies), breed in the boreal and arctic climate zones (Piersma *et al.* 1996). They have precocial young that forage for themselves from hatching onwards, leading to high muscular activity and prolonged exposure to outdoor conditions. This ontogenetic mode should lead to a high energy expenditure (Chapter 2, Schekkerman & Visser 2001), especially in the cold and shelter-poor arctic tundra (Norton 1973). Thus, arctic shorebird chicks may need more food to achieve growth than young birds at temperate latitudes and also more than parent-fed chicks in the Arctic. At the same time, small shorebird chicks are not yet homeothermic at low ambient temperatures (Chappell 1980, Beintema & Visser 1989a, Visser & Ricklefs 1993, Visser 1998), hence a cold climate increases their need for parental brooding, and shortens potential feeding time. At first sight therefore, self-feeding precociality seems to be a mode of development not agreeing well with the arctic environment. Nevertheless, shorebirds constitute a large proportion of arctic tundra bird communities (Chernov 1985, Boertmann *et al.* 1991, Troy 1996), and arctic species show the highest growth rates among shorebirds (Beintema and Visser 1989a, Schekkerman *et al.* 1998, Chapter 4), so the thermal difficulties must be offset in some way. It has been suggested that compared to lower latitudes, insect food is more abundant in the arctic summer (e.g. Lack 1968, Salomonsen 1972, Andreev 1999), while the continuous summer daylight provides extra feeding time (Karplus 1952, Lack 1954). To make full use of this, chicks could have developed thermal adaptations to reduce the need for brooding at low temperatures (e.g. Koskimies & Lahti 1964, Chappell 1980). To date, no study has evaluated these hypotheses in an integrated way.

We studied prefledging energy expenditure and time budgets of Red Knot *Calidris canutus* chicks in the Siberian Arctic, to test whether they are indeed energetically expensive. The Red Knot is one of the most northerly breeding shorebirds, confined to arctic tundra and polar desert (Piersma & Davidson 1992, Tomkovich & Soloviev 1996), yet shows one of the fastest growth rates found in this group. We compare energy expenditure and time budgets of knot chicks and the abundance of their invertebrate prey with those of temperate shorebirds in grasslands in The Netherlands (Schekkerman & Visser 2001, Schekkerman & Beintema 2007, Chapter 6)), and use a simulation model based on the comparative data to evaluate the three hypothetical mechanisms for enabling Red Knots to grow so fast despite the energetic challenge posed by their environment.

MATERIALS AND METHODS

Study area

We studied breeding Red Knots at Cape Sterlegov on the Taimyr Peninsula, Siberia (75°25'N, 89°08'E) from 10 June to 12 August 1994 (Tulp *et al.* 1998). The study area consisted of 12 km^2 of arctic tundra (*sensu* Chernov 1985) bordering the Kara Sea, between 0 and 50 m a.s.l. Vegetation was dominated by mosses and lichens with a considerable proportion of bare ground in the form of clay medallions or 'frost boils', and with a denser cover of grasses and sedges in moister parts. Some scattered stone ridges and rocky outcrops were present. Several small marshes and streams drained the area.

Red Knot growth and behaviour

Fourteen Red Knot nests and 25 broods were found by flushing incubating birds from underfoot or by rope-dragging, and by traversing the study area intensively after hatching started. Any chicks encountered were ringed, and most accompanying adults (males) were trapped and individually colour-ringed. Two adult males, one captured on the nest and the other on 1-day old chicks, were fitted with a radio transmitter (Holohil, Canada, type BD-2, 1.8 g) glued to feather bases on the lower back (Warnock & Warnock 1993). The transmitters were used to relocate broods for doubly labelled water experiments (see below) and behavioural observations. One tagged male lost its chicks to predators after a week, but the other fledged two young.

Throughout the prefledging period, chicks were recaptured whenever possible to record their growth (103 recaptures of 37 chicks from 13 broods). Weights were determined with spring balances, accurate to 0.1-1 g. Body mass growth was described by a logistic curve. Because the exact age of many chicks was unknown as they had already left the nest when first encountered, the logistic growth rate parameter was estimated from mass increments of chicks captured at least twice (Schoener & Schoener 1978, Ricklefs 1983), using nonlinear regression. Hatchling mass was measured in the field, and the asymptote was fixed at 120 g, the mean mass of first-year Red Knots wintering in West Africa (Wymenga *et al.* 1992).

To analyse environmental effects on growth rate, mass increments were used of chicks at least a day old and captured twice at intervals of 1-5 days (mean 1.7 days, SD=1.23, N=87). To make growth rates at different ages comparable, observed mass increments were divided by those predicted from the logistic equation at the given starting mass and recapture interval. These indices were regressed on average temperature and food availability during the interval. By treating chick and brood as random variables in linear mixed models (Byrk & Raudenbusch 1992), we took into account that the data represent three nested error levels (multiple observations on several chicks from the same brood). The program MLN (Institute of Education 1995) was used for model fitting. To avoid bias due to possible effects of doubly labelled water trials on growth rate, mass increments during such measurements were excluded.

Time budget observations were made on three different broods for a total of 62.6 h, covering all hours of the day and chick ages 0-13 days. Observations were made from 100-300 m distance, using a telescope. Behaviour of the male and chicks was recorded every minute, distinguishing between brooding, foraging, and other behaviours (including rest, preening, walking, and alarm). Broods formed the recording unit, as the alternation between brooding and foraging was highly synchronised among brood mates. The dependence of the proportion of time that chicks were brooded on chick age and temperature was analysed by logistic regression. Observations lasting longer than 3 h were divided into sampling units of 1.5-3 (mean 2.3) h, to standardise lengths and get an appropriate mean value for temperature, which often changed significantly over a few hours.

Energy expenditure

Measurements of daily energy expenditure (DEE, kJ/d) of free-living chicks were made using the doubly labelled water (DLW) method (Lifson & McClintock 1966, Speakman 1997). Captured chicks were injected subcutaneously in the ventral region with 0.15-0.50 ml of DLW consisting of 32 atom-% D_2O and 68 atom-% $H_2{}^{18}O$. They were kept warm in a bag or box for an equilibration period of 0.75-1 h and structural measurements and weight were recorded. Four to six 10-15 μL blood samples were then collected from veins in the leg or wing, into glass capillary tubes, which were flame-sealed within minutes. Chicks were released into the field and recaptured after 19.0-25.6 h (mean 23.3 h, SD=1.5, N=15), a second set of blood samples and measurements was taken. In three chicks, additional blood samples were collected before injection with DLW to measure background isotope levels. Since broods roamed widely over the tundra and were often difficult to relocate, most DLW measurements were taken on chicks of the radio-tagged males. A few measurements were made on chicks of non-tagged males. At most three measurements were taken on (two) individual chicks, separated by 3-6 day intervals.

$^2H/^1H$ and $^{18}O/^{16}O$ ratios in the blood samples were analysed with a SIRA 9 isotope ratio mass spectrometer at the Centre for Isotope Research, Groningen, following procedures described in Visser & Schekkerman (1999). Analyses were done in duplicate, and a third capillary was analysed if the two measurements differed by more than 2%. Background concentrations were 0.0143 atom-% for ^2H and 0.1989 atom-% for ^{18}O (N=3). We calculated CO_2-production according to equation 34 in Lifson & McClintock (1966), with fractionation factors for ^{18}O and ^2H taken from Speakman (1997), and a value of 0.13 for the fraction of water loss occurring by evaporation:

$$rCO_2 \text{ (l/d)} = (N / 2.078 \times (k_o - k_d) - 0.13 \times 0.0249 \times N \times k_d) \times 22.4,$$

in which N is the size of the body water pool (mol), and k_o and k_d the fractional turnover rates of ^{18}O and ^2H, respectively, as calculated from the isotope measurements. In a validation study on chicks of two related shorebirds, Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus,* this method gave an average error of 0% (Visser & Schekkerman 1999). The errors (range -13% to +16%) were unrelated to growth rate, indicating that the method is accurate in chicks growing as fast as 20%/day. Because some DLW was occasionally lost by leakage during injection, N was not estimated from isotope dilution but from the relation between percentage water content and the fraction of adult mass attained, based on analysis of carcasses of lapwing and godwit chicks (Schekkerman & Visser 2001, Chapter 2). DEE was calculated from $r\mathrm{CO}_2$ using an energy equivalent of 27.33 kJ/l CO_2 (Gessaman & Nagy 1988).

Total daily Metabolised Energy (ME) was calculated by adding energy deposited into new tissue (E_{tis}) to DEE in case the animal gained weight over the measurement period, and set equal to DEE if no weight gain occurred. E_{tis} was estimated as the increment of the product of body mass and energy density. The latter was taken as:

ED (kJ/g) = $4.38 + 3.21\ M/M_{ad}$ (M=chick body mass, g, M_{ad} =adult mass, 120 g),

based on carcass analysis of chicks of Northern Lapwing and Black-tailed Godwit (Schekkerman & Visser 2001). Dependence of DEE and ME on body mass, growth rate and weather was analysed by fitting linear mixed models, containing chick and brood as random variables, to the log-transformed data.

Weather and arthropod abundance

Three-hourly observations of air temperature (T_a,°C), wind speed and cloud cover were obtained from a weather station 7 km from our study site. From 3 July onwards, operative temperature (T_e,°C) was automatically recorded every five minutes, using a blackened copper sphere (Ø 4 cm) placed 10 cm above the ground. T_e integrates air temperature and solar radiation and provides a better description of the thermal environment than air temperature alone (Walsberg & Weathers 1983). Daily means of T_e were linearly related to mean T_a at the weather station: $T_e = 1.23\ T_a + 1.96$ (R^2=0.82, $F_{1,34}$=156.6, $P<0.001$). Occurrence of rain and snowfall was recorded daily.

Abundance of surface-active arthropods which constitute the food of Red Knot chicks was measured in five modified pitfall traps placed at 20 m intervals in moderately dry nanopolygonal tundra (the habitat where most of the broods were encountered). Traps consisted of white plastic jars (Ø 10 cm, 13.5 cm deep), filled with 1-2 cm of water and a drop of detergent to break the surface tension. Two crossed mesh screens of 40 by 50 cm, topped with a plastic funnel opening into a transparent jar, were placed over the pitfalls. In addition to surface-active animals, this structure caught low-flying invertebrates which hit the screens and crawled either downwards into the pitfall or upwards into the jar. Compared to ordinary pitfalls, the modified traps caught more small Chironomid midges and Linyphiid spiders but similar numbers of other groups (Tulp *et al*. 1998). Arthropods were collected daily between 22:00 h and 24:00 h, and preserved in 4% formalin. They were later identified to family or (sub)order (Hymenoptera, Collembola) and body length was measured (to nearest 0.5 mm if ≤5 mm; to 1 mm if larger). Dry weights were estimated from group-specific length-weight relationships (Rogers *et al*. 1977, Schekkerman unpublished). Arthropod abundance data were log-transformed before analysis. Because mites (Acari) and springtails (Collembola) are too small to be important prey for chicks, they were not taken into account in most analyses.

Comparison with temperate shorebird chicks

Data on Red Knots (growing from 13.7 g at hatching to 108 g at fledging in 18 days) were compared with those for three temperate-breeding wader species, Northern Lapwing (growing from 17.5 to 142 g in 23 days), Black-tailed Godwit (28.6 to 201 g in 25 days) and Common Redshank *Tringa totanus* (15.6 to 109 g in 23 days), studied in grassland reserves in the Netherlands using similar methods. DLW measurements of energy expenditure of lapwing and godwit chicks were made at Baarn (52°12'N, 05°19'E) in 1993-95 (Schekkerman & Visser 2001). Time budget observations were made from hides in 0.4-0.8 ha enclosures surrounded by a low fence which allowed the free-living adults but not their chicks to freely leave and enter. Observations were made in Flevoland (52°24'N, 5°40'E) in 1981 and 1984 (Beintema & Visser 1989a) and at Baarn in 1992-95 (Chapter 5), and totalled 992 h for godwits, 644 h for lapwing and 44 h for redshank (10, 10 and 2 broods respectively). Dependence of brooding proportions on chick mass or age and weather variables was analysed using logistic regression, in the same way as in Red Knots. T_e was measured with the same equipment at Baarn as in Siberia; temperatures measured in Flevoland were converted to T_e using regression models incorporating air temperature, time of day and solar radiation, based on data from Baarn.

Abundance of surface-active arthropods was measured in a grassland reserve at Baarn between 3 May and 7 June 1994 (i.e. the period in which most chicks are present), using the same type and number of modified pitfall traps as in Taimyr, and identical methods of collection, identification and analysis.

RESULTS

Weather and arthropod availability

Upon our arrival on 11 June, the tundra was still 98% snow-covered. Average air temperature remained below 0°C until 18 June. After 19 June (90%), snow cover declined rapidly to 50% on 21 June and 10% on 26 June. Mean daily air temperature (T_a ± SD) was -0.7 ± 3.1°C (range -4.9 to 4.4) in the arrival period of Red Knots (10-22 June), 4.5 ± 4.4°C (range 0.9 to 14.2) during incubation (23 June-13 July) and 0.9 ± 1.8°C (range −0.9 to 7.1) during chick-rearing (14 July to 10 Aug). Mean operative temperature (T_e) in the latter period was 2.8 ± 2.8°C (range 0.2 to 10.1), and mist, drizzle or rain occurred on many days. Daily average wind speed was mostly between 3 and 7 m/s, with peaks up to 8-10 m/s.

Diptera were the most abundant arthropod group caught in the modified pitfall traps at Cape Sterlegov (60% of total number), followed by Araneae (23%), Hymenoptera (12%) and Coleoptera (5%). Daily total number and dry mass were strongly correlated (log-transformed data, 3 July-10 August, r_{34}=0.95, $P<0.001$), and biomass was further used as an index of arthropod availability.

Regression analysis showed a strong non-linear dependence of trapped biomass (excluding mites and springtails) on operative temperature (T_e: $F_{1,34}$=62.2, $P<0.001$; T_e^2: $F_{1,33}$=41.6, $P<0.001$; R^2=0.65), with a steep decline at T_e<4-5°C (fig. 3.1). The occurrence of rain or (wet) snowfall reduced arthropod activity (if the only explanatory variable: $F_{1,34}$=60.1, $P<0.001$, R^2 =0.38), even when entered into the model after temperature ($F_{1,32}$=13.3, P=0.001; R^2=0.74). A negative effect of wind speed (in isolation: $F_{1,34}$=32.3, $P<0.001$, R^2 =0.20) was no longer significant after temperature and rain were included

($F_{1,31}$=0.37, P=0.55). Inclusion of date and date^2 after T_e and precipitation further improved the model ($F_{2,30}$=5.80, P=0.007; final R^2 =0.81), indicating that independently of weather there was a unimodal seasonal trend in arthropod activity. Predicted arthropod availability peaked on 11 July when weather effects were not taken into account (fig. 3.1a), but on 16 July when these were included in the regression model.

The average size-density distributions of trapped arthropods were similar between Cape Sterlegov and a Dutch grassland managed as a meadowbird reserve (fig. 3.2). Because arthropods ≥8 mm were more abundant in The Netherlands, mean daily trapped biomass (mean ± SD: 19.0 ± 12.0 mg/d/trap, N=29 days) was higher here than at Cape Sterlegov (11.7±13.0 mg/d/trap, N=31 days; t-test on ln-transformed data, t_{58}=3.03, P=0.002). With mites and springtails included, this difference was even larger (Cape Sterlegov 11.7 ±13.0 mg/d/trap, Netherlands 31.7 ± 18.2 mg/d/trap, fig. 3.2).

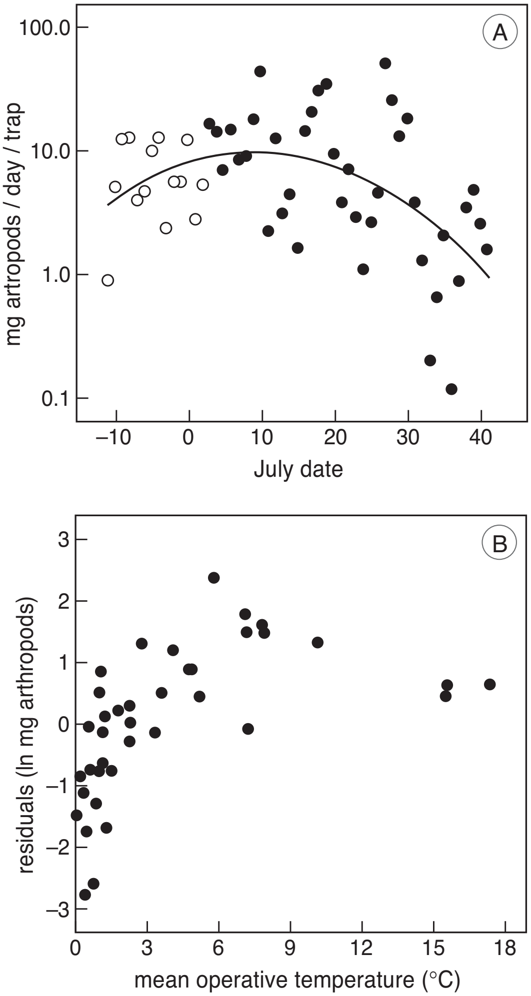
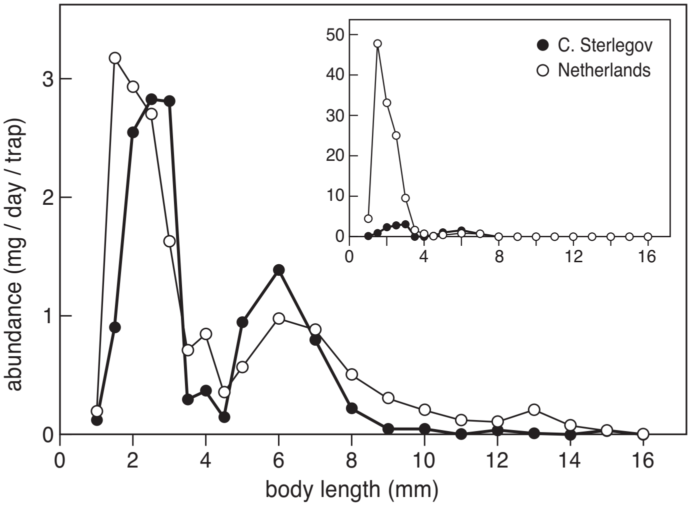


FIGURE 3.1. Daily arthropod dry biomass caught in pitfall traps in relation to date (A; open dots show biomass before 3 July when no measurements of T_e were made; ln(mg)= 0.082 date −0.0037 date^2 +3.58, $F_{2,33}$=8.07, P=0.0014, R^2=0.33) and operative temperature T_e (B; residuals from parabolic relationship in A).

FIGURE 3.2. Size-abundance distributions of arthropods caught in modified pitfall traps at Cape Sterlegov and in a grassland reserve in The Netherlands. Large graph: mites (Acari) and springtails (Collembola) excluded; inset: all groups included.



Red Knot breeding phenology and growth

Red Knots were present in the study area upon our arrival (11 June), but new migrants arrived until at least 19 June. Most of the 14 nests (12 4-egg, two 3-egg clutches) found in the intensive study area were depredated by an Arctic Fox *Alopex lagopus*, but 11 additional broods were later found within its borders (estimated density ≤2 pairs/km^2), and 14 outside it. Based on direct observations, flotation of eggs and biometrics of young, eggs hatched between 14 and 28 July. The median hatching date was 17 July, corresponding to a first-egg date of 22 June (4 d laying, 20-21 d incubation). Incubation was shared between sexes but females deserted at hatching, and joined into small flocks, which disappeared one or two weeks later. Males attended the chicks alone, until a few days after fledging. Westward migration occurred in late July and early August, and most Red Knots, including juveniles, had left the area by 10 August.

The mean mass of hatchlings still in the nest was 13.7 ± 0.5 g (N=8). Chicks fledged when 17-20 days old, weighing 87-114 g at last capture. Body mass growth in relation to age (t, days) was best described as:

$$M\ (g) = 120 / (1 + 8.23\ e^{-0.24\ t})$$

(SE of rate parameter K_L=0.03, R^2=0.93, N=103 intervals from 37 chicks in 13 broods, mass range 13-107 g). Conversion of KL to the Gompertz' growth rate parameter (Ricklefs 1983) yields K_G=0.163, which is 1.9 times the value predicted for a 120 g shorebird by Beintema & Visser (1989). Hence, Red Knots are very fast growing shorebirds.

The index of chick growth rate (growth observed / expected at the observed mass) was positively related to mean operative temperature during the recapture interval (likelihood ratio test, χ^2_1=16.4, P<0.001, N=87 intervals for 33 chicks in 12 broods). The relationship seemed non-linear and ln(T_e) gave a slightly better fit than T_e (χ^2_1=19.7, P<0.001). Adding the (negative) effect of precipitation to that of temperature further improved the model (χ^2_1=5.23, P=0.02). However, the best fit was obtained with the logarithm of mean daily arthropod biomass trapped in the pitfalls as the independent variable (χ^2_1=49.7, P<0.001, fig. 3.3). This model was not improved by the inclusion of T_e (χ^2_1 =1.36, P=0.24) or precipitation (χ^2_1=0.44, P=0.51), whereas adding arthropod availability to a model including both ln(T_e) and precipitation resulted in a highly significant improvement (χ^2_1=27.7, P<0.001). This indicates that not only weather-induced variation in arthropod availability affected growth, but also seasonal variation. One chick lost an exceptional 8 g in a day (growth index -3.2, fig. 3.3); because this occurred on a cold day with very low arthropod activity, omitting this data point did not change the results.

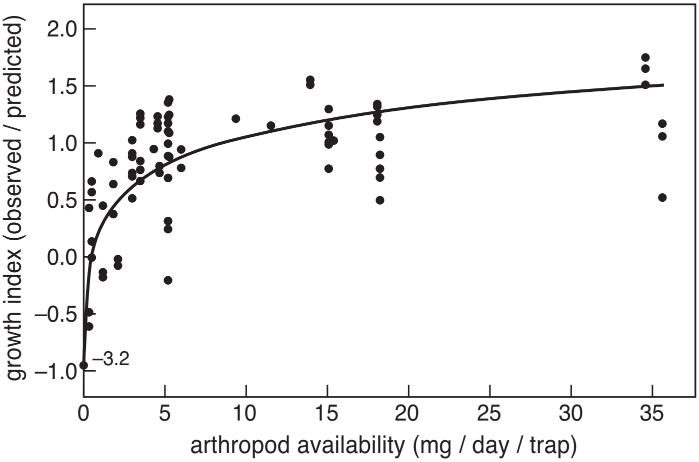


FIGURE 3.3. Relationship between the growth index of Red Knot chicks (growth observed / predicted at observed mass) and mean daily arthropod biomass trapped during the interval between successive captures. The lowest observed growth index was –3.2; this point was shifted to -0.95 to fit into the frame. Regression equation: y = -0.311 (SE=0.194) + 0.306 ln(x) (SE=0.036); further statistics in text.

Time budgets

Of 62.6 observation hours, Red Knot chicks were brooded by the parent during 39%. In chicks older than 8-9 days, brooding was observed only rarely. Of the remaining time, chicks spent 98% foraging (other behaviours slightly underestimated as preening, resting and alarm events lasting <1 minute were not recorded). Brooding was thus the key determinant of feeding time for young chicks.

The time that chicks were brooded declined strongly with increasing body mass and T_e (table 3.1). In addition to these effects, brooding occurred most often between

TABLE 3.1. Logistic regression analysis of the proportion of time that Red Knot chicks were brooded by a parent (B), in relation to body mass, temperature, time of day and wind speed. Results are given for forward stepwise inclusion of significant variables. Two-way interactions were also tested, but not significant (all P>0.13). 'Night' was defined as the period 22:00-04:00 h. Coefficients are for logit (B)=ln(B/(1-B)).

variables in model	change in *df*	change in deviance	P	coefficient logit (B)	(SE)
constant				5.22	(3.43)
chick mass (g)	1	6.83	0.009	−0.160	(0.085)
T_e (°C)	1	4.92	0.027	−0.281	(0.176)
if 'night'	1	5.54	0.019	2.67	(1.26)
wind speed (m/s)	1	0.03	0.86	n.s.	
residual	22	5.17			
total	25	19.0			

22:00 and 04:00 h. Wind speed had no discernible effect on brooding, nor were any interaction effects significant. Results were very similar when age was used as independent variable instead of body mass.

At the same mass (or age) and temperature, Red Knot chicks were brooded less than temperate shorebird chicks observed in the Netherlands (fig. 3.4, table 3.2). The difference between Red Knot and Common Redshank (smallest samples), was close to significance ('species' added to logistic model with mass, T_e and 'night': χ^2_1=3.62, P=0.057); it was significant when age was used instead of mass (χ^2_1=4.47, P=0.035), due to the knots' faster growth. Differences with Black-tailed Godwit (χ^2_1=11.0, P<0.001) and Northern Lapwing (χ^2_1=29.9, P<0.001) were highly significant, despite the knots' smaller size.

Energy expenditure

Fifteen DLW experiments were completed on 10 chicks from 5 broods. During 12 of these the chicks gained mass at an average rate of 5.3 g/d (SE=0.3), or a growth index of 0.82 (SE=0.05) compared to the average growth curve. The slower growth of DLW-injected chicks is explained by measurements being made on days with relatively low food availability: the average growth index predicted from arthropod abundance on trial days was 0.81. Three chicks lost 3.0-4.1 g/d during DLW trials (average growth index = -0.63, SE=0.13); this was more than predicted from arthropod availability (-0.06).

The power function describing daily energy expenditure (DEE, kJ/d) in relation to body mass (M, g) was:

$$\log(DEE) = 0.492 + 1.078 \log(M)$$

(SE_{B0}=0.163, SE_{B1}=0.091, likelihood ratio test, χ^2_1=34,9, P<0.001) (fig. 3.5). Including average T_e (°C) during the DLW trial improved this model: DEE decreased with increasing T_e:

$$\log(DEE) = 0.442 + 1.129 \log(M) - 0.023 T_e$$

(SE_{B0}=0.145, SE_{B1}=0.083, SE_{B2}=0.010, χ^2_1=4.16, P=0.041). Wind speed (P=0.75), rainfall (P=0.31), arthropod availability (P=0.92) and growth rate over the measurement interval (P=0.12) had no significant effect on DEE in addition to that of body mass.

Daily metabolised energy (ME, kJ/d, DEE plus energy deposited into tissues (E_{tis}) if the chick gained mass) was related to body mass as:

$$\log(ME) = 0.837 + 0.916 \log(M)$$

(SE_{B0}=0.130, SE_{B1} 0.073 χ^2_1=36.7, $P<0.001$, fig. 3.5). In contrast to DEE, there was no significant effect of temperature on ME in addition to that of mass (χ^2_1=0.01, P=0.92); apparently the increase in DEE at low T_e was compensated by reduced growth (lower E_{tis}). Wind speed (P=0.14), rainfall (P=0.69), arthropod activity (P=0.75) or growth rate (P=0.76) did not affect ME either.

Total energy requirements of a Red Knot chick fledging at Cape Sterlegov were estimated by summing daily estimates of ME over the 18-day fledging period. At each age, mass predicted from the average growth curve and mean T_e over the period of chicks' presence (2.8 °C) were inserted into the regression equation relating DEE to mass and T_e. Predicted mass and growth rate were also used to estimate E_{tis}, which was added to DEE to obtain ME. ME increased at a decelerating rate from 65 kJ/d at hatching to 494 kJ/d at fledging (108 g). Total ME over this period amounted to 5285 kJ, of which 14% was made up by E_{tis} and the remaining 86% by DEE, including basal metabolism and costs of thermoregulation, activity, and biochemical synthesis.

FIGURE 3.4. Comparison of proportional brooding time in relation to body mass at the same temperature (A) and to operative temperature at the same age (B) for chicks of Red Knot (Kn), Common Redshank (Re), Black-tailed Godwit (Go), and Northern Lapwing (La). Lines show predictions from logistic regression models (tables 3.1 and 3.2) during dry weather in daytime.

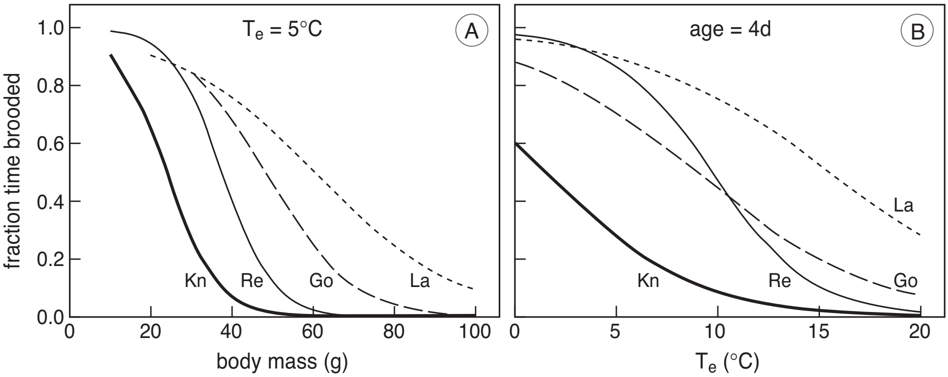
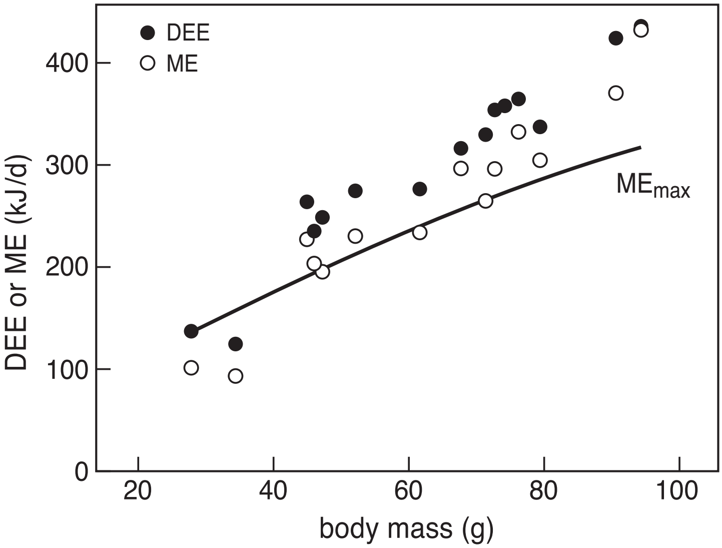


TABLE 3.2. Logistic regression parameters for proportion brooding time (B) in chicks of three shorebird species studied in temperate grasslands (the Netherlands). All observations were made in daylight as chicks were inactive at night (*c.* 22:00-06:00 h). Rainfall was set to 1 if rain fell during ≥10 % of the time (too few wet observations were made to include this variable for Red Knots). Coefficients are given for logit (B)=ln(B/(1-B)). All coefficients were significant at $P<0.05$, except that for rain in Common Redshank ($\chi^2_1=3.5$, P=0.06)

variable	Black-tailed Godwit		Northern Lapwing		Common Redshank	
	coefficient	(SE)	coefficient	(SE)	coefficient	(SE)
constant	5.512	(0.548)	4.373	(0.430)	8.02	(3.70)
mass	−0.094	(0.011)	−0.0556	(0.0071)	−0.160	(0.093)
T_e	−0.199	(0.022)	−0.202	(0.021)	−0.401	(0.197)
rain	0.661	(0.252)	1.122	(0.275)	2.41	(1.34)
residual deviance	181.4		145.1		3.5	
total deviance	561.4		375.5		24.1	
total *df*	991		643		43	

FIGURE 3.5. Daily energy expenditure (DEE, kJ/d) and metabolised energy (ME, kJ/d) of Red Knot chicks in relation to body mass (M, g). Allometric regression equations: DEE = 3.105 $M^{1.078}$; ME = 6.871 $M^{0.916}$ (further statistics in text). For comparison, an allometric relationship between ME and M in birds and mammals under energy-demanding conditions (Kirkwood 1993; ME_{max}) is also shown.



DISCUSSION

High energy requirements in arctic-breeding shorebirds

ME of Red Knot chicks exceeded an allometric prediction of 'maximum' ME based on various birds and mammals under energy-demanding conditions (Kirkwood 1983), in 14 out of 15 cases (fig. 3.5). Weathers (1992) reviewed prefledging energy requirements in 30 bird species, and derived a predictive equation for total metabolised energy (TME) over the prefledging period. The largest (absolute) difference between observed and predicted values in Weathers's (1992) sample was 40%, while our value for knots is 89% above the prediction.

Two factors likely to contribute to these high energy requirements are the Red Knots' precocial lifestyle and the cold climate. The studies reviewed by Weathers (1992) included mostly temperate-breeding birds with parent-fed young. Self-feeding chicks exhibit high muscular activity, which should increase energy expenditure compared to parent-fed nestlings in any climate. In temperate-breeding Black-tailed Godwits and Northern Lapwings, TME was 28% and 45% higher than Weathers' (1992) prediction (Schekkerman & Visser 2001). That mass-corrected DEE was yet *c.* 80% higher in knots is most probably accounted for by the much lower temperature in the Arctic. The largest differences between observed and expected TME found by Weathers (1992) occurred in the arctic-breeding Dunlin *Calidris alpina* (+40%, Norton 1970) and Arctic Tern *Sterna paradisaea* (+35%, Klaassen *et al.* 1989). Subsequent measurements on American Golden Plover *Pluvialis dominica* (+52%, Visser *et al*. unpublished data), Black-legged Kittiwake *Rissa tridactyla* (+35%, Gabrielsen *et al*. 1992), Little Auk *Alle alle* (+35%, Konarzewski *et al*. 1993) and Wilson's Storm-Petrel (+148%, Obst & Nagy 1993), also revealed high TME in polar environments.

Fast growth in the Arctic – why, and how?

In addition to elevating energy requirements, low temperatures increase a shorebird chick's need for parental brooding, thereby reducing time available for foraging (Chappell 1980, Beintema & Visser 1989a, Visser & Ricklefs 1993). In response, arctic-breeding shorebirds might have evolved a slower growth rate which reduces the chicks' daily energy requirements (Lack 1968, Ricklefs 1984, Drent & Klaassen 1989, Klaassen *et al.* 1992), but in fact they show the opposite: arctic-breeding shorebirds tend to have higher growth rates than temperate species (Beintema & Visser 1989a, Schekkerman *et al.* 1998a, this study). An ultimate explanation for this is that the length of the season suitable for growth is short in the Arctic, constrained at the start by snow melt and at the end by declining temperature or food availability (e.g. Holmes 1966a,b, 1972, Carey 1986, see below). In addition, fast growth itself may help chicks to overcome the energetic difficulties, because size is an important thermal characteristic of animals (Visser 1998).

At the proximate level, the fast growth shows that there must be factors compensating for the thermal difficulties faced by arctic chicks. Below, we explore the applicability to the Red Knot's case of three (not mutually exclusive) mechanisms that have been proposed.

Day length - The continuous arctic summer daylight does not impose an inactive period on visual foragers, and this would allow chicks to increase their daily energy intake and hence growth rate compared to lower latitudes (Karplus 1952, Lack 1954, Kvist & Lindström 2000). Red Knots, however, did not take full advantage of this: chicks were brooded more between 22:00 h and 04:00 h than during other times, irrespective of temperature. Although the sun never set until early August, light levels were noticeably lower 'at night', and activity and harvestability of arthropods may have been reduced. Alternatively, young knots may need more sleep than can be accommodated into daytime brooding bouts, and may have taken extra resting time 'at night'. Adult birds of 12 species observed in arctic summer conditions slept 3.7 h per day on average (Amlaner & Ball 1983). Compared to a 8 h dark period in spring in The Netherlands, this would still allow for a 27% increase in feeding time. Growing animals like young knots may need more sleep, but how much is unclear.

Cold-hardiness – Arctic chicks may have evolved structural or metabolic adaptations that reduce the need for parental brooding and thus increase foraging time (Chappell 1980). Indeed, Red Knots were brooded less than chicks of three temperate shorebird species at the same mass and temperature, and they became thermally independent earlier. This agrees with the finding that hatchlings of ducks with a northern breeding distribution are cold-hardier than those of more southern species (Koskimies & Lahti 1964). Increased cold-hardiness may be achieved in three ways: (1) arctic chicks may be better isolated, e.g. have thicker down, (2) they may tolerate lower body temperatures than temperate chicks (Norton 1973, West & Norton 1975, Chappell 1980), (3) they may be able to elevate metabolic rate higher above basal level under cold stress. The latter two mechanisms might be facilitated by a reduced risk of infection and disease in arctic compared to temperate environments, allowing arctic chicks to compromise immunodefence for increased metabolic performance (Piersma 1997).

We cannot distinguish between these mechanisms on the basis of our data. The few literature data on operational body temperatures in shorebirds do not support hypothesis (2): Chicks of three arctic *Calidris* sandpipers gave distress calls and became sluggish at a core temperature of *c.* 30°C (Norton 1973), while chicks of the temperate Common Redshank voluntarily tolerated 27°C, and Common Snipe *Gallinago gallinago* cooled down to 24-26°C without signs of distress (Myhre & Steen 1979). Subtropical Crowned Plover *Vanellus coronatus* chicks also voluntarily operated at body temperatures down to 30°C (Brown & Downs 2002). Evidence for mechanisms (1) and (3) was found in young Eiders *Somateria mollissima* (Koskimies & Lahti 1964, Steen *et al.* 1989). Mechanism (3) would contribute to the chicks' high energy expenditure, so that the gain in feeding time will be partly offset by a concomitant increase in energy requirements.

Food availability - Alternative to increased foraging time, energy intake rate during foraging might be higher in the summer tundra than in temperate environments (Lack 1968, MacLean & Pitelka 1971, Salomonsen 1972, Andreev 2000). Our pitfall samples revealed a lower rather than a higher mean daily biomass of surface-active arthropods at Cape Sterlegov than in a temperate meadow. Because arthropod abundance and activity may vary between years as well as between sites, this finding cannot be generalised, but Red Knots at Cape Sterlegov did not experience a higher abundance of food than Dutch shorebird chicks in 1994. However, they might still have achieved a higher intake rate, if prey were more easily detected or captured. This could be a result of the simpler structure of the tundra vegetation, compared to a temperate grassland sward, or of a larger proportion of slow-moving or wingless arthropods at high latitudes (*cf.* Chernov 1985).

Comparative simulation model

To explore the relative importance of the explanations discussed above, we constructed a comparative model in which the (metabolisable) energy intake rate during foraging, required to meet the daily demands for maintenance and growth, was simulated on the basis of our measurements of ME and foraging time, for Red Knots at Cape Sterlegov and for Common Redshank in the Netherlands. Redshank are similar in adult mass (109 g) to knot (120 g), but grow more slowly. If the simulated intake rate of knots exceeds that of redshank, better feeding conditions must be invoked to explain the fast growth of arctic knot chicks; if not, the higher metabolism can be met solely by an increase in foraging time. By changing values for temperature, day length, growth rate and cold-hardiness, we also explored which factors are most important in maximising feeding time in the Arctic. We considered that without a dark period of forced inactivity, sleep requirements may reduce foraging time unless they can be fitted within brooding bouts. Equations and assumptions of the model are detailed in the Appendix.

The model predicts potential foraging time (FT), energy requirements (ME) and required intake rate (RI) for each day during an 18-day prefledging period. Total FT over this period for a Common Redshank in The Netherlands was indexed at 100%. Allowing for 6 h of sleep, predicted total FT for Red Knots in Taimyr is very similar (102%, without sleep 128%, fig. 3.6). Despite their greater cold-hardiness 0-4 d old knots have less foraging time than redshank due to the low temperature; later this is reversed but the knots' advantage depends strongly on their need for sleep.

If a redshank chick were to live at 3°C under a temperate day length of 16 h, its total FT over 18 days would be reduced to 46% of that at 15°C (fig. 3.6). With continuous daylight and 6 h/d of sleep at 3°C (i.e. after an imaginary translocation to the Arctic), the redshank's FT would be 61% of that in the Netherlands. Assigning a knot's growth rate to this chick increases FT (to 82%), because it is larger than a redshank at each age and thus requires less brooding. Finally, the larger cold-hardiness of a knot increases FT to 102%. The effects of growth rate and cold-hardiness partly substitute each other: when a redshank chick at 3°C and an 18 h day is given knot cold-hardiness, FT increases from 61% to 95%, and increasing growth rate only adds a further 7%.

Total ME over 18 days is 160% higher in Red Knots than in Common Redshank, causing a large difference in required foraging intake rate (RI, fig. 3.7). Because ME strongly depends on body mass, much of this difference is caused by the knots' higher growth rate. Assuming knot growth rate for redshank, and allowing for a coupling between growth rate and RMR elevating ME by a further 9% (see Appendix), the difference in TME reduces to 46%. This would bring RI of redshank very close to that of knots if these need no time for sleep (fig. 3.7), but it is more likely that knots need a higher intake rate.

We conclude from this simulation that Red Knot chicks can grow up successfully in the Arctic because of a combination of factors. Cold-hardiness and growth rate are

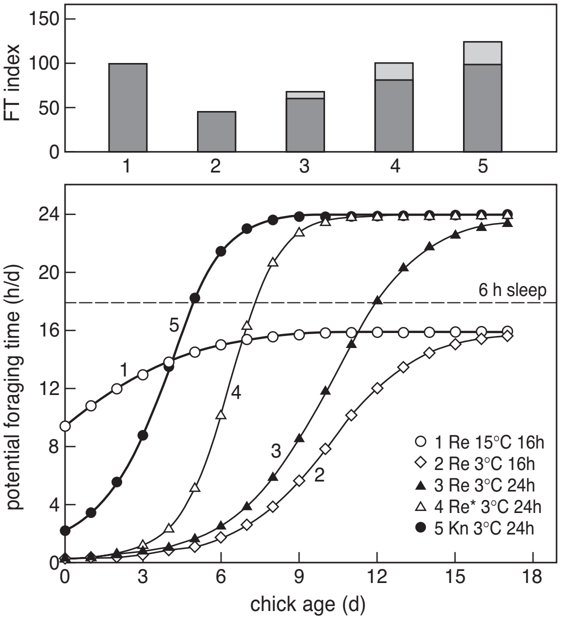


FIGURE 3.6. Simulated potential foraging time (FT) in relation to age (bottom panel) of Red Knot and Common Redshank chicks, and of imaginary chicks with mixed species/environment characters (see Appendix for model details). Starting with a redshank in a temperate environment (1), T_e was changed from 15°C to 3°C (2), then day length from 16 to 24 h/d (3), and then growth rate (4) and finally cold-hardiness (5) to a Red Knot's. Horizontal broken line indicates maximum potential foraging time under the assumption of 6 h needed for sleep. Upper panel shows the resulting total foraging time over 18 days (area under curves), indexed to 100 for a temperate redshank (dark grey: with 6 h/d sleep; light grey: extra if no sleep required). Kn=Red Knot; Re=Common Redshank; Re*=redshank with knot growth rate.

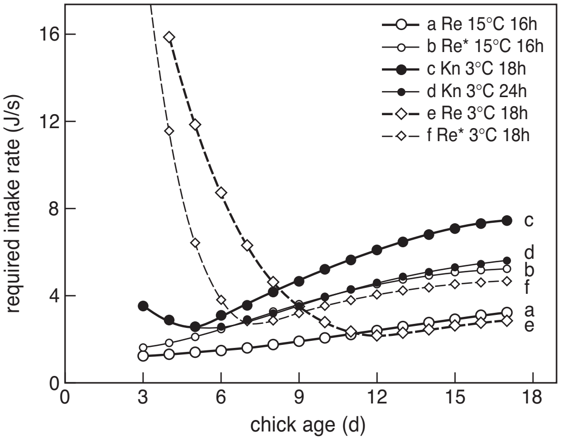


FIGURE 3.7. Simulated required (metabolisable) intake rate in relation to age for Red Knot and Common Redshank chicks, and of imaginary chicks with mixed species/environment characters. Lines a-d: Knot need a higher intake rate than redshank, but the difference is strongly dependent on time needed for sleep. Lines e-f: Without a knot's greater cold-hardiness, young (≤5 d) chicks would need extremely high intake rates. Kn=Red Knot; Re=Common Redshank; Re*=redshank with knot growth rate.

important factors compensating for feeding time lost due to low temperatures. Continuous daylight also contributes, but how much depends strongly on the unknown time needed for sleep. The resulting total feeding time differs little between Red Knots and Common Redshanks in their natural environment. However, because knots expend more energy, a higher foraging intake rate must still be invoked to fully explain their fast growth. Since we trapped fewer rather than more surface-active invertebrates in our arctic study area than in a temperate grassland, this seems more likely due to an easier detection or capture of invertebrates in the tundra than to a difference in abundance.

Fast growth and increased cold-hardiness, if achieved by a higher peak metabolism, contribute to the high energy requirements of Red Knots. Although these traits therefore have costs as well as benefits, the cold-hardiness of knots seems essential for survival during early life, when feeding time is constrained by the need for parental brooding. If translocated to the Arctic, redshank chicks up to 5-6 days old would need an excessively high intake rate, unlikely to be achieved in the field (fig. 3.7). Assigning knot growth rate to such a chick shortens this critical period by a few days, but does not eliminate it. Lipid stores of neonate shorebird chicks allow for no more than *c.* 1 day of survival at peak metabolic rate (Visser & Ricklefs 1995). Only introducing the greater cold-hardiness of young Red Knots reduces RI to feasible levels throughout.

Effects of weather, food availability and breeding phenology on growth rate

Despite their high overall growth rate, Red Knot chicks did at times run into energetic problems, indicated by the strong relationship between growth rate and weather. Three non-exclusive mechanisms may underlie this. (1) At low temperatures young chicks were brooded more, and thus had less time available for foraging. However, weather also affected growth rate of older, thermally independent chicks. (2) DEE but not ME increased with falling temperature, indicating that on cold days energy is allocated to thermoregulation at the expense of tissue formation. (3) Low temperature and precipitation strongly reduced the activity of surface-dwelling invertebrates. Though we did not measure intake rate directly, it is likely that this represents a reduction in prey availability for chicks: on cold days invertebrates were hardly visible on the tundra surface (*cf.* Holmes 1966a). Our finding that trapped arthropod biomass predicted chick growth rate better than weather variables suggests that food availability was the most important factor, and was adequately described by the pitfall samples.

The strong relationship between chick growth rate and arthropod availability points to the importance of timing reproduction so that the chicks can make full use of the summer peak in insect abundance (e.g. Hurd & Pitelka 1954, Holmes 1966a,b, Nettleship 1974, Tulp & Schekkerman 2008). The median hatching date of Red Knots in our study fell 6 days after the observed peak date of arthropod availability, though only 1 day after the predicted seasonal maximum corrected for temperature effects. However, the simulation model showed that required intake rate is higher for chicks older than 10 days than for newly hatched young (fig. 3.7), hence peaked at a time when food availability was already declining. The seasonal curve for arthropod availability dropped below 5 mg/d/trap, a level below which growth rate declined seriously, on 28 July (fig. 3.1), a week before chicks born on the median hatching date fledged.

Near the median fledging date, the predicted growth rate index dropped below 50%. Unless older chicks exploit additional food sources unavailable to young ones (but we did not see them e.g. probe for buried larvae), Red Knots might therefore increase their offspring's growth rate and survival by laying earlier. In 1994 however, they could hardly have done so, because only 10% and 50% of the tundra had become snow-free on the earliest and median laying dates respectively. Clutches can only be initiated after suitable nest sites have become exposed, and shorebird nests in small snow-free patches incur high predation risk (Byrkjedal 1980). Similar constraints on fitting laying date to the seasonal peak in food availability for the young were reported for arctic-breeding geese (Sedinger & Raveling 1986, Lepage *et al.* 1998, Madsen *et al.* 1998). Such a mismatch will contribute to selection for a strategy of maximising growth rate at the expense of high energy requirements. While this strategy may be common in arctic birds (Klaassen & Drent 1991, see Fortin *et al.* 2000 for another precocial example), in the small and extremely northerly breeding Red Knot the energetic consequences show up particularly clearly.

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REFERENCES

- Amlaner C.J. & N.J. Ball 1983. A synthesis of sleep in wild birds. Behaviour 87: 85-119.
- Andreev A.V. 2000. Energetics and survival of birds in extreme environments. Ostrich 70: 13-22.
- Beintema A.J. & Visser G.H. 1989a. The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77: 181-192.
- Beintema A.J. & G.H. Visser 1989b. Growth parameters of charadriiform chicks. Ardea 77: 169-180.
- Boertmann D., H.Meltofte & M.Forchhammer 1991. Population densities of birds in central northeast Greenland. Dansk Ornitologiske Forenings Tidsskrift 85: 151-160.
- Brown M. & C.T. Downs 2002. Development of homeothermy in hatchling crowned plovers *Vanellus coronatus*. Journal of Thermal Biology 27:95-101.
- Byrk A.S. & S.W. Raudenbush 1992. Hierarchical linear models, application and data analysis. Sage, London.
- Byrkjedal I. 1980. Nest predation in relation to snow cover – a possible factor influencing the start of breeding in shorebirds. Ornis Scandinavica 11: 249-252.
- Carey C. 1986. Avian reproduction in cold climates. Proceedings of the International Ornithological Congress XIX, Ottawa: 2708-2715.
- Chappell M.A. 1980. Thermal energetics of chicks of arctic-breeding shorebirds. Comparative & Biochemical Physiology 65A: 311-317.
- Chernov Y.I. 1985. The living tundra. Cambridge University Press, Cambridge.
- Fortin D., G. Gauthier & J. Larochelle 2000. Body temperature and resting behaviour of Greater Snow Goose goslings in the High Arctic. Condor 102: 163-171.
- Gabrielsen G.W., M, Klaassen & F. Mehlum 1992. Energetics of Black-legged Kittwake chicks. Ardea 80: 29-40.
- Gessaman A. & K.A. Nagy 1988. Energy metabolism: errors in gas excange conversion factors. Physiological Zoology 61: 507-513.
- Holmes R.T. 1966a. Feeding ecology of the Red-backed Sandpiper (*Calidris alpina)* in Arctic Alaska. Ecology 47: 32-45.
- Holmes R.T. 1966b. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper *(Calidris alpina*) in Northern Alaska. Condor 68: 3-46.
- Holmes R.T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. American Midland Naturalist 87: 472-491.
- Hurd P.D., & F.A. Pitelka 1954. The role of insects in the economy of certain Arctic Alaskan birds. Proceedings 3rd Alaskan Science Conference: 136-137.
- Institute of Education 1995. MLn. Institute of Education, London.
- Karplus M. 1952. Bird activity in the continuous daylight of arctic summer. Ecology 33: 129-134.
- Kirkwood J.K. 1983. A limit to metabolisable energy intake in mammals and birds. Comparative & Biochemical Physiology 75A: 1-3.
- Klaassen M., C. Bech, D. Masman & G. Slagsvold 1989. Growth and energetics of Arctic Tern chicks (*Sterna paradisaea*). Auk 106: 240-248.
- Klaassen M. & R.H. Drent 1991. An analysis of hatchling resting metabolism: in search of ecological correlates that explain deviations from allometric relations. Condor 93: 612-629.
- Klaassen M., B. Zwaan, P. Heslenfeld, P. Lucas & B. Luijckx 1992. Growth rate associated changes in the energy requirements of tern chicks. Ardea 80: 19-28.

- Konarzewski M., J.R.E. Taylor & G.W. Gabrielsen 1993. Chick energy requirements and adult energy expenditures of Dovekies (*Alle alle*). Auk 110: 343-353.
- Koskimies J. & L. Lahti 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution of ten species of European ducks. Physiological Zoology 65: 803-814.
- Kvist A. & Å. Lindström 2000. Maximum daily energy intake: it takes time to lift the metabolic ceiling. Physiological & Biochemical Zoology 73: 30-36.
- Lack D. 1954. The natural regulation of animal numbers. Oxford University Press, London.
- Lack D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Lepage D., G. Gauthier & A. Reed 1998. Seasonal variation in growth of Greater Snow Goose goslings: the role of food supply. Oecologia 114: 226-235.
- Lifson N., R. McClintock 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. Journal of Theoretical Biology 12: 46-74.
- Madsen J., T. Bregneballe, J. Frikke & J.-B. Kristensen 1998. Correlates of predator abundance with snow and ice conditions and their role in determining timing of nesting and breeding success in Svalbard Light-bellied Brent Geese *Branta bernicla hrota*. Norsk Polarinstuts Skrifter 200: 221-234.
- MacLean S.F. & F.A. Pitelka 1971. Seasonal patterns of abundance of tundra arthropods near Barrow. Arctic 24: 19-40.
- Myhre K. & J.B. Steen 1979. Body temperature and aspects of behavioural temperature regulation in some neonate subarctic and arctic birds. Ornis Scandinavica 10: 1-9.
- Nettleship D.N. 1974. The breeding of the Knot *Calidris canutus* at Hazen Camp, Ellesmere Island, N.W.T. Polarforschung 44: 8-26.
- Norton D.W. 1970. Thermal regimes of nests and bioenergetics of chick growth in the Dunlin (*Calidris alpina*). at Barrow, Alaska. M.Sc. thesis, University of Alaska, Fairbanks.
- Norton D.W. 1973. Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph.D. Thesis, University of Alaska, Fairbanks.
- Obst B.S., K.A. Nagy 1993. Stomach oil and the energy budget of Wilson's Storm-petrel nestlings. Condor 95: 792-805.
- Piersma T. 1997. Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? Oikos 80: 623-631.
- Piersma T., N.C. Davidson (eds) 1992. The migration of knots. Wader Study Group Bull 64, Suppl: 1-209.
- Piersma T., J. van Gils & P. Wiersma 1996. Family Scolopacidae (sandpipers, snipes and phalaropes). In J. del Hoyo, A. Elliot & J. Sargatal (eds). Handbook of the birds of the world. Vol. 3 : 444-553. Lynx Edicions, Barcelona.
- Ricklefs R.E. 1983. Avian postnatal development. In D.S. Farner, J.R. King & K.C. Parkes (eds), Avian biology, Vol. 7: 1-83. Academic Press, New York.
- Ricklefs R.E. 1984. The optimization of growth rate in altricial birds. Ecology 65: 1602-1616.
- Rogers L.E., L.R. Buschbom & C.R. Watson 1977. Length-weight relationships for shrubsteppe invertebrates. Annals of the Entomological Society of America 70: 51-53.
- Salomonsen F. 1972. Zoogeographical and ecological problems in arctic birds. Proceedings International Ornithological Congress XV, The Hague: 25-77.
- Sedinger J.S. & D.G. Raveling 1986. Timing of nesting in Canada Geese in relation to the phenology and availability of their food plants. Journal of Animal Ecology 55: 1083-1102.

- Schekkerman H., G. Nehls, H. Hötker, P.S. Tomkovich, W. Kania, P. Chylarecki, M. Soloviev & M. van Roomen 1998. Growth of Little Stint *Calidris minuta* chicks on the Taimyr Peninsula, Siberia. Bird Study 45: 77-84.
- Schekkerman H., M. van Roomen & L.G. Underhill 1998. Growth, behaviour of broods and weather-related variation in breeding productivity of Curlew Sandpipers *Calidris ferruginea*. Ardea 86: 153-186.
- Schekkerman H. & G.H. Visser 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. Auk 118:944-957.
- Schoener T.W. & A. Schoener 1978. Estimating and interpreting body mass growth in *Anolis* lizards. Copeia 1978: 390-405.
- Speakman J.R. 1997. Doubly labelled water. Theory and practice. Chapman and Hall, London.
- Steen J.B., H. Grav, B. Borch-Iohnsen & G.W. Gabrielsen 1989. Strategies of homeothermy in Eider ducklings (*Somateria mollissima*). In C. Bech, & W. Reinertsen (eds), Physiology of cold adaptation in birds. NATO ASI Series A, Vol. 173: 361-370. Plenum Press, New York.
- Tomkovich P.S. & M.Y. Soloviev 1996. Distribution, migration and biometrics of Knots *Calidris canutus canutus* on Taimyr, Siberia. Ardea 84: 85-98.
- Troy D. 1996. Population dynamics of breeding shorebirds in Arctic Alaska. International Wader Studies 8: 15-27.
- Tulp I., H. Schekkerman, T. Piersma, J. Jukema, P. de Goeij & J. van de Kam 1998. Breeding waders at Cape Sterlegova, northern Taimyr, in 1994. WIWO-report 61, Working Group International Wetland and Waterbird Research, Zeist, The Netherlands.
- Tulp I. & H. Schekkerman 2008. Weather- and season-related variation in the abundance of tundra arthropods: hindcasting the effect of climate change on prey availability for arctic birds. Arctic 61: 48-60.
- Visser G.H. 1998. Development of temperature regulation. In J.M. Starck & R.E. Ricklefs (eds), Avian growth and development: 117-156. Oxford University Press, New York.
- Visser G.H. & R.E. Ricklefs 1993. Development of temperature regulation in shorebirds. Physiological Zoology 66: 771-792.
- Visser G.H. & R.E. Ricklefs 1995. Relationship between body composition and homeothermy in neonates of precocial and semiprecocial birds. Auk 112: 192-200.
- Visser G.H. & H. Schekkerman 1999. Validation of the doubly labelled water method in precocial birds: the importance of assumptions concerning evaporative water loss. Physiological & Biochemical Zoology 72:740-749.
- Walsberg G.E. & W.W. Weathers 1986. A simple technique for estimating operative environmental temperature. Journal of Thermal Biology 11: 67-72.
- Warnock N., S.E. Warnock 1993. Attachment of radio-transmitters to sandpipers: review and methods. Wader Study Group Bulletin 70: 28-30.
- Weathers W.W. 1992. Scaling nestling energy requirements. Ibis 134: 142-153.
- West G.C. & D.W. Norton 1975. Metabolic adaptations of tundra birds. In F.J. Vernberg (ed.). Physiological adaptation to the environment: 301-329. Intext Education Publishers, New York.
- Wymenga E., M. Engelmoer, E. Smit & T.M. van Spanje 1992. Geographical origin and migration of waders wintering in West Africa. In W. Altenburg, E. Wymenga & L. Zwarts (eds.), Ornithological importance of the coastal wetlands of Guinea-Bissau: 23-52. WIWO-report 26. Working Group International Wetland and Waterbird Research, Zeist.

Appendix: simulation model

The simulation model predicts body mass, foraging time, energy requirements and required metabolisable energy intake of Red Knot and Common Redshank chicks during an 18 day fledging period, on the basis of growth, time budget and metabolism data reported in this paper or from the literature. We distinguished two environments differing in daylength (D, h/d) and operative temperature (T_e, °C): arctic (D=24 h/d, T_e=3°C, data from Cape Sterlegov) and temperate (D=16 h/d, T_e=15 °C, data from The Netherlands, May-June 1992-1995).

At each age t, body mass (M, g) of chicks was predicted from a logistic growth curve:

knot: $M = 120 / [1 + 8.23\ e^{-0.240\ t}]$ (this study) (1a)

redshank: $M = 109 / [1 + 6.17\ e^{-0.137\ t}]$ (from Beintema and Visser 1989b) (1b)

The proportion of daylight time that chicks were brooded by a parent (B) was calculated by inserting mass and T_e into logistic regression equations derived from our time budget observations (tables 3.1 and 3.2). As too few observations with rain were made for knots to estimate its effect on brooding time, we used the equations for dry weather in both species:

knot: $\mathrm{logit}(B) = 5.22 - 0.160\ M + 0.027\ T_e$ (2a)

redshank: $\mathrm{logit}(B) = 8.02 - 0.160\ M + 0.401\ T_e$ (2b)

Potential foraging time (FT, h/d) was calculated as day length minus brooding time. Redshank chicks do not forage during darkness (unpubl. obs.). We made calculations including and excluding the condition that chicks need 6 hours of sleep each day, to show the effect of this requirement. We assumed that temperate chicks fit this into the 8 h night, while arctic chicks sleep whenever brooded and reduce foraging time only if daily brooding time is less than time required for sleep (i.e., if B < 0.25):

arctic: $FT = 24 - (24\ B)$ if $B \geq 0.25$; $F = D - S$ if $B < 0.25$ (3a)

temperate: $FT = 16 - (16\ B)$ (3b)

In a balanced budget, total metabolisable energy intake over the hours spent foraging equals energy metabolised over the entire 24 h period (ME, kJ/d). Hence, required metabolisable energy intake rate while foraging (RI, J/s) at each age was calculated as:

$$RI = ME / (3.6\ FT) \quad (4)$$

ME is the sum of daily energy expenditure as measured with DLW (DEE, kJ/d) and energy incorporated into tissue (E_{tis}, kJ/d):

$$ME = DEE + E_{tis} \quad \text{if } E_{tis} > 0 \text{ ; } ME = DEE \quad \text{if } E_{tis} \leq 0 \quad (5)$$

E_{tis} was calculated as the daily increment of the product of body mass and energy density, the latter estimated from the fraction of adult mass attained (see Methods):

knot: $E_{tis} = M_{t+1}\,[4.38 + 3.21\,M_{t+1} / 120] - M_t\,[4.38 + 3.21\,M_t / 120]$ (6a)
redshank: $E_{tis} = M_{t+1}\,[4.38 + 3.21\,M_{t+1} / 109] - M_t\,[4.38 + 3.21\,M_t / 109]$ (6b)

For DEE of knot chicks, we used the equation derived in Results, inserting T_e=3°C. Because DEE was not measured in Common Redshank, we used the mass-DEE relationship for Black-Tailed Godwit chicks (Schekkerman & Visser 2001). This relation did not differ significantly from that for Northern Lapwings, despite considerable differences in age at the same mass, hence we assumed that it applies to redshank as well. The equation is based on DLW measurements made at a mean T_e of 15°C.

knot: $DEE = 2.630\,M^{1.129}$ (7a)
redshank: $DEE = 1.549\,M^{1.092}$ (7b)

No predictions of ME and RI were made at ages 0-2 d, because regression equations overestimate energy requirements during this period (there is a rapid increase in metabolism over the first 3 days, Visser & Ricklefs 1993), and because the contribution of energy stores present in the hatchling (yolk) was not taken into account.

The effect of environmental and physiological variables on FT and RI was explored by exchanging environment and species parameters. For instance, a redshank chick was virtually transposed into the Arctic by changing daylength from 16 to 24 h/d and T_e from 15°C to 3° C. Subsequently exchanging equation 2b for 2a shows the effect on foraging time of a knot's greater cold-hardiness than that of a redshank.

When comparing ME and RI between the species, the difference in growth rate must be taken into account, as ME depends strongly on body mass. We did so by inserting the Red Knot growth equation (1a) into the model for Common Redshank. Klaassen & Drent (1991) proposed that Resting Metabolic Rate in hatchling birds is coupled to growth rate, which implies that redshank could only grow at a knot's rate at the expense of an increase in RMR. A rough estimate of this additional effect would be a 9% increase of ME (based on fig. 4 in Klaassen & Drent 1991, a 75% higher growth rate would lead to a 29% increase in RMR which is *c.* 33% of ME in temperate shorebird chicks, Schekkerman & Visser 2001).

Growth, behaviour of broods, and weather-related variation in breeding productivity of Curlew Sandpipers *Calidris ferruginea*

4

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1. Growth and survival of chicks and movements of broods were studied in Curlew Sandpipers *Calidris ferruginea* in NE Taimyr, Siberia, in 1991. Effects of weather on chick survival and breeding productivity were examined by correlating data on annual variation in the proportion of juveniles among wintering birds in South Africa with 18 years of summer weather records from the core of the Taimyr breeding area.

2. Breeding was synchronised, 73% of 30 clutches hatching during 10-15 July. Nests were contageously distributed in dry frost-heaved tundra. Broods were tended by females only and moved from the nest sites to low-lying wet areas up to 2.4 km away during the first week of life. Here, they often formed aggregations of 2-6 broods with females cooperating in predator defence.

3. Chicks fledged in 14-16 days, and body mass growth was best described by a logistic curve. The growth rate constant K_L was 0.314, which is high compared to similar-sized waders studied elsewhere. Growth rate was reduced during cold weather, as was the availability of surface-active arthropods which form the main food source for chicks.

4. In 1991 (a lemming peak year), both clutch and chick survival were high, and breeding productivity was *c.* 2 fledglings per female. After allowing for an effect of three-yearly cyclic variation in lemming abundance on predation of eggs and young by arctic foxes and skuas, interannual variation in breeding productivity was positively correlated with mean temperature in Taimyr during 11-20 July, the period when most young chicks are present in the tundra. We found no correlations between productivity and weather during the pre-laying period, in contrast to several studies on arctic-breeding geese.

5. Weather thus seems to have effects on chick survival both widespread and large enough to be detected in the wintering areas, and the combination of (inferred) predation pressure and weather conditions during the fledging period explains a large part of the variation in breeding productivity found in this species.

INTRODUCTION

The Curlew Sandpiper *Calidris ferruginea* is a breeding bird of arctic tundras in northern Siberia, between the Yamal Peninsula in the west and the Chukchi Peninsula in the east. Aspects of its breeding biology have been described by Portenko (1959), Holmes & Pitelka (1964), Tomkovich (1988) and Tomkovich *et al*. (1994), but growth and survival of chicks and behaviour of family parties have not been intensively studied.

The species is a long-distance migrant wintering in (sub)tropical and south-temperate latitudes from Africa to New Zealand (Hayman *et al.* 1986). It has been noted for the highly fluctuating numbers of juvenile birds occurring on autumn migration in western Europe (Stanley & Minton 1972, Roselaar 1979) and in winter in southern Africa (Summers & Underhill 1987). These fluctuations show a three-year periodicity which is synchronous with fluctuations in juvenile output in other wader species and Brent Geese *Branta bernicla* breeding on the Taimyr Peninsula (Underhill *et al.* 1989). The 'prey-switching hypothesis' (Roselaar 1979, Summers 1986, Dhont 1987), explains this pattern from a switch made by predators from a diet of lemmings to birds' eggs and young after a decrease in lemming abundance. During a three-year lemming cycle, breeding success is poor in the year after a lemming peak, when lemming numbers have decreased sharply and predators are abundant following good reproduction. In the next two years predation on birds is much lower, due to an increase of lemmings combined with low numbers of predators in the second, and an abundance of lemmings in the third year. The hypothesis has received support with respect to waders from a comparative field study in Taimyr during a lemming peak and a lemming low year (Underhill *et al.* 1993).

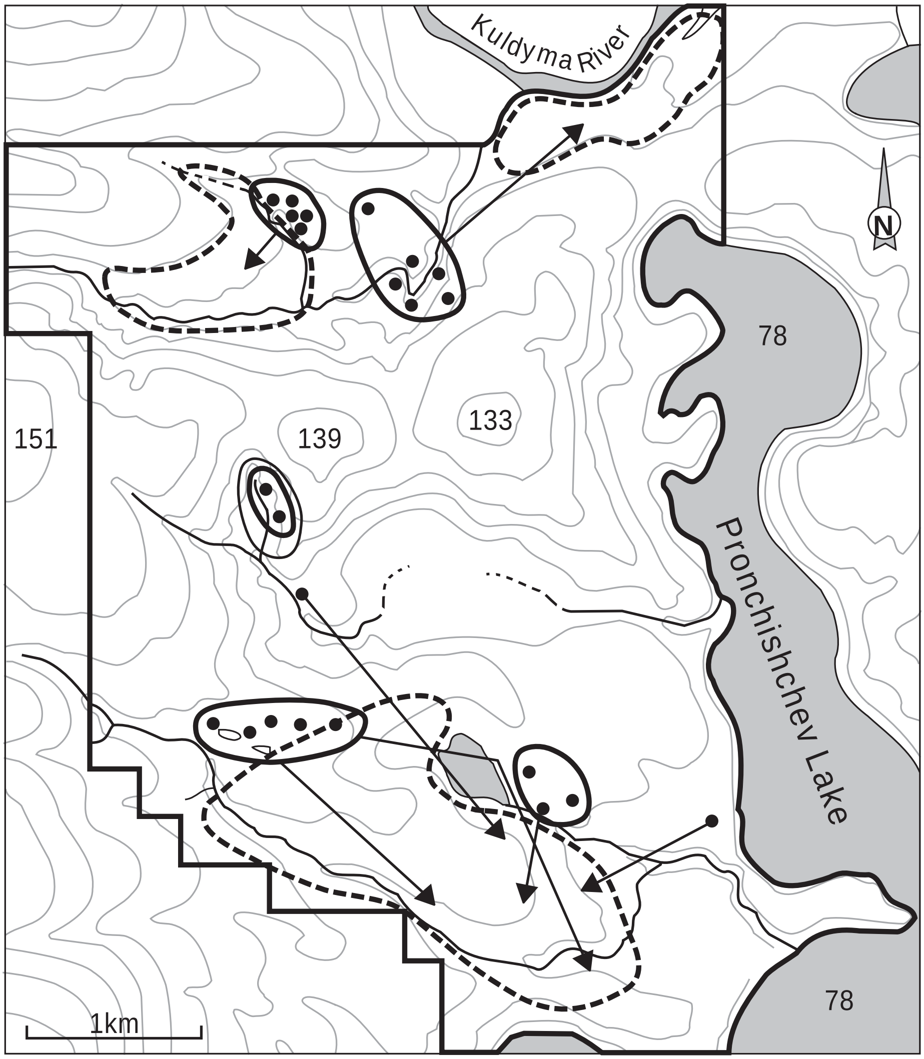
However, breeding success is not guaranteed when predation is low (Dhont 1987). In arctic-breeding geese, energy stores upon arrival or feeding conditions during the pre-laying period may affect clutch size (Ebbinge 1989, 1990, Ganter & Cooke 1996). For waders, in which clutch size is less variable than in geese, weather during the fledging period may be an important factor, by influencing survival of the chicks.

In this paper, we describe growth and development of chicks and reproductive success of Curlew Sandpipers in a study area on the Taimyr Peninsula in 1991, a lemming peak year (Underhill *et al*. 1993). In this year, we found a correlation between growth rate of chicks and local weather conditions. Since growth rates may be reflected in chick survival, we extended the scope of the study by analysing data on Curlew Sandpiper breeding productivity, recorded in a non-breeding area over 18 years, for correlations with weather conditions during the main chick-rearing period.

Study area

Curlew Sandpipers were studied between 15 June and 8 August 1991, near Pronchishchev Lake in the northeastern part of the Taimyr Peninsula (75°16'N, 112°28'E), 30 km from the Laptev Sea. The area consisted of moderately dry hilly arctic tundra (Chernov 1985), drained by three small rivers (fig. 4.1). Watersheds and upper parts of slopes were generally well-drained and consisted of sparsely vegetated frost-heaved and frost-boiled tundra. Wetter areas occurred on the lower parts of slopes and in marshes in valleys and on level parts of watersheds (see Schekkerman & Van Roomen 1995 for a

FIGURE 4.1. The intensive study area west of the northern extension of Pronchishchev Lake, with locations of Curlew Sandpiper nests (dots). The thick unbroken line delineates the area covered during searches for broods later in the season (15.6 km²); the northernmost and southernmost 0.8 km² were not searched for nests. Broods from clusters of nests within the solid circles joined into loose aggregations and were found within the areas bounded by broken lines during most of the fledging period. Arrows denote general direction of movement from nesting to brood-rearing areas. Heights (in m a.s.l.) of the lake and the two highest points in the study area, as well as 10-m altitude contours, are given.



detailed description). Snow cover dropped below 90 % on 21 June, and reached 50% on 27 June and 5% on 3 July (Underhill *et al*. 1993).

1991 was a lemming peak year in the study area, with lemming densities of up to 400 animals/ha. Snowy Owls *Nyctea scandiaca*, Pomarine *Stercorarius pomarinus* and Long-tailed Skuas *S. longicaudus,* and Arctic Foxes *Alopex lagopus* fed almost exclusively on the abundant lemmings and reproduced well (Underhill *et al.* 1993).

METHODS

Field procedures

Curlew Sandpiper nests were located in a 14 km^2 area by watching females return after disturbance. Nests were marked, and clutch size and egg measurements were recorded. Eggs were marked and weighed at intervals to determine the rate of mass loss during incubation and the date of clutch completion (Underhill *et al*. 1993). Incubating females were trapped with a small clap-net. They were weighed and measured, and given a combination of metal and colour-rings for individual recognition. Most were also dyed with picric acid on the left underwing.

Survival of clutches was monitored by visits to nests at approximately three day intervals. Towards hatching, nests were visited more frequently to establish their outcome and ring the chicks. After hatching, a slightly extended (15.6 km^2; fig. 4.1) area was regularly searched for females with broods. Chicks were (re)captured whenever possible, and body mass (spring balance), wing length (maximum chord, after the primary tips had appeared), length of bill (exposed culmen) and tarsus were measured.

Locations of broods were recorded relative to a 250×250 m grid with the aid of a 1:25000 map. The presence of chicks was fairly easily ascertained from the alarm behaviour of the females. Minimum brood size was determined by observation from a distance or from captures, though often the number of chicks alive could not be assessed with certainty. When repeatedly fewer chicks were observed in a brood than expected from the number of eggs hatched, it was assumed that the missing chicks had died. In this way, chicks were classified as ‘alive’, ‘fate unknown’, or ‘dead’ at five-day age intervals.

Maximum and minimum air temperatures were recorded daily at the camp, using a thermometer placed 1 cm above the ground and shaded from the sun. The abundance and activity of surface-dwelling tundra arthropods was monitored using 10 pitfall traps, placed along a 100 m transect in moderately dry tundra. They were emptied every day around midnight in June and on average every three days in July, and the animals were classified into broad taxonomical groups and counted (Underhill *et al.* 1993).

Growth

Logistic growth curves were fitted to data from chicks of which the age was known to within 24 h. Because of lack of independence between data points obtained from individual chicks, approximate standard errors for the parameter estimates were derived using the jack-knife technique, by serial exclusion of individual chicks from the dataset (Sokal & Rohlf 1981). The growth curves (mainly those for bill and wing length) were used to estimate the hatching date for broods that were found only after hatching.

To analyse the relationship between growth and weather conditions, growth rates were calculated for chicks captured and measured twice within a period of at least two and at most seven days. To take account of the sigmoid shape of the growth curve and make growth rates comparable for different ages, they were converted to a 'growth index' by dividing the observed growth by the growth expected on the basis of the average logistic curve for all individuals (equation 19 in Schoener & Schoener 1978). The indices were then regressed on the average temperature during the interval between captures. Because chicks from the same brood do not produce independent observations, hierarchical linear modelling was applied (Byrk & Raudenbusch 1992), which takes into account that chicks and broods represent different error levels in the data. The program MLN (Institute of Education 1995) was used for model fitting.

Long-term weather and productivity data

Data of Curlew Sandpiper breeding productivity, measured as the percentage of first-year birds in samples trapped for ringing on wintering grounds in South Africa, were taken from Summers & Underhill (1987), Underhill (1990), and Underhill & Oatley (1995). To investigate relationships between breeding productivity and weather conditions on the breeding grounds, data for 1977-1990 were available from a weather station near the delta of the Pyasina River in NW Taimyr (73°34'N, 86°15'E). These comprised daily minimum and maximum temperature (averaged to daily mean temperature), daily mean wind speed (based on four measurements per day), and daily precipitation in June, July and August of each year. In addition, the date at which snow depth decreased to 50% of the value on 1 June was used as an estimate of the timing of snow melt. After 1990, data recording at the weather station was discontinued, but additional temperature measurements for 1990-1994 were available from Lydia Bay, 50 km to the NE (B.S. Ebbinge & B. Spaans unpubl.). In June-July 1990, daily mean temperatures here and at the weather station showed a tight correlation (r_{48}=0.92, P<0.001), and a linear regression equation was used to convert Lydia Bay temperatures to weather station values for 1991-1994. Wind speed data were not available for these years.

Relations between summer weather and the proportion of first-year birds in the winter population were explored using logistic regression. Levels of 'inferred predation pressure' (IPP) were based on qualitative descriptions of lemming abundance on the Taimyr Peninsula (Summers & Underhill 1987, Ryabitsev 1993, Yurlov 1993, Tomkovich 1994a,b, 1995). They show a pronounced periodicity with low IPP during a lemming peak every third year, followed by a decline in lemming abundance leading to high IPP. We assumed that predation exerts its greatest effect on productivity in the egg stage, while weather is more likely to affect the survival of chicks, and incorporated IPP into the regression models before assessing the effects of weather. Both linear and quadratic effects of weather variables (mean temperature and mean wind speed during 10-day periods) were considered, as well as their interactions with IPP, using a forward selection procedure. Analyses were carried out with Genstat 5.3 (Genstat 5 Committee 1993).

RESULTS

Breeding density, phenology and breeding success in 1991

Curlew Sandpipers were already present at Pronchishchev Lake upon our arrival on 15 June. Twenty-five nests were found in the study area in 1991, as well as 10 additional broods of which 6-8 were assumed to have hatched within its boundaries. With a density of *c.* 2.3 breeding females per km^2, the Curlew Sandpiper was the most abundant wader species in the area (Underhill *et al.* 1993).

Twenty-four (77%) of 31 clutches were completed between 19 and 27 June, and the remainder between 3 and 8 July (median date 25 June). Hatching took place between 10 and 26 July, with 73% of 30 clutches hatching between 10 and 15 July, and with the peak and median on 12 July. Twenty-two clutches contained four eggs, and one each contained three, two and one egg (mean clutch size 3.76, SD=0.72, N=25).

Curlew Sandpiper chicks fledged at an average age of 15 days. Out of six broods checked at 13 days of age, none were able to fly ≥20 m; these figures were 1/3, 2/3 and 5/5 for broods of 14, 15 and 16 days, respectively. Females incubated and tended broods alone. Males were last observed singing on 2 July, and none were seen in the study area after 10 July. Females stayed with the brood until shortly after fledging; they were seen accompanying fledged chicks of 16 (5×), 17 (2×) and 20 days of age. Small numbers of westward-migrating females (either failed breeders or successful birds migrating ahead of their young) were seen between 20 July and 5 August, and small flocks of migrant juveniles from 27 July onwards until our departure on 8 August.

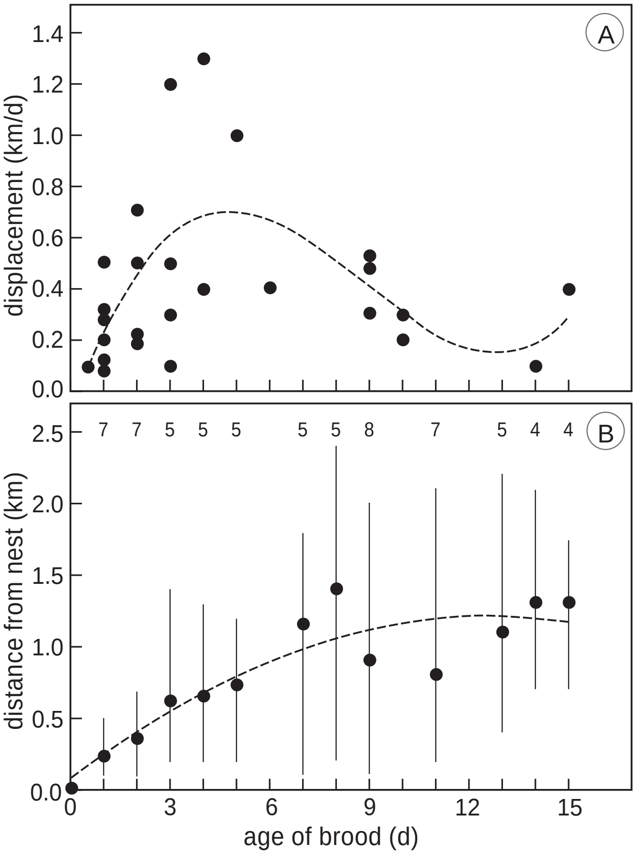
Nest success was high, none of 25 clutches being lost to predation or desertion during 235 nest-days. More than 90% of the eggs hatched; part of the few losses were due to eggs being damaged during handling. The fate of a large proportion of the chicks was not known, but chick mortality seemed to be highest during the first five days after hatching (Schekkerman & Van Roomen 1995). Of 23 Curlew Sandpiper broods hatched before 25 July, 10 (43%) produced at least one fledged juvenile (total number fledged between 18 and 74). If it is assumed that all chicks alive at day 10 survived to fledging, at least 16 broods (70%) were successful and 28-79 chicks fledged, 1.2-3.4 per breeding female. Since some broods may have moved beyond the limits of the study area, brood survival may have been underestimated and productivity was probably around two chicks per breeding female.

Habitat choice and brood movements

Nests were situated in moderately dry ‘frost-heaved’ tundra, usually in the vicinity of a patch of wetter tundra with growth of sedges, where the females did most of their foraging. Nest sites were highly aggregated (fig. 4.1), much more so than the distribution of dry tundra would suggest, and corresponding to the distribution of snow-free patches early in the season.

Broods left the nest within a day after hatching. In general, they moved away from the nesting sites to lower-lying moist areas where they remained during the latter part of the fledging period (fig. 4.1). Distances between brood locations on consecutive days were small during the first few days, but increased rapidly to a maximum at three to five days of age (fig. 4.2a). Thereafter, movements became less directional, resulting

FIGURE 4.2. Displacements of Curlew Sandpiper broods in relation to age. A: Straight-line distances between locations observed on consecutive days. B: Mean and range of distances between brood locations and nest site (sample sizes given on top). Broken lines show polynomial curves fitted to lead the eye, using hierarchical linear modeling (taking into account that broods provided multiple data points); both quadratic (B) and cubic (A) terms were significant at $P<0.05$.



in smaller daily displacements. Distances between the locations of broods and their nest site did not increase further after the first week (fig. 4.2b). The maximum observed distance from the nest was 2.4 km, but some broods may have left the study area and moved beyond our attention.

The areas used by broods during the latter half of the fledging period were generally open with little microrelief, allowing free views of the surroundings. They were located mainly on the lower, less steep slopes of hills and in wide valleys. In contrast to the nesting habitat, these sites were rather wet, with sedges dominating the aspect of the vegetation.

In the brood-rearing areas, broods tended to join into loose aggregations with other families of Curlew Sandpipers and, less often, other species. Out of 78 observations of broods, 43 (65%) were in aggregations, which usually consisted of 2-4 (maximum 6) families. Distances between broods in aggregations varied between approximately 10 and 200 m, but were rarely so small that chicks intermingled. The females collaborated when alarming for and mobbing skuas and human observers, although each returned to her own chicks when predators were not in the vicinity. No exchange of ringed chicks between broods was observed. The composition of aggregations was rather stable, but changes in number and identity of participants did occur. Although they often involved females which had bred close together, they were not formed directly after hatching, but mainly between four and seven days later, coinciding with the arrival in the brood-rearing areas (table 4.1). Several aggregations included one or two broods of Turnstone *Arenaria interpres* (5×), Little Stint *Calidris minuta* (4×), or Sanderling *C. alba* (1×).

Growth and weather conditions

Body mass showed little change during the first day after hatching (fig. 4.3). Therefore, chick masses determined in the first 24 h after hatching were not used in fitting the mass growth curve. Bill length and tarsus length increased from the first day onwards, and all data were used. Logistic curves produced a slightly better description of the slow initial increase in body mass and bill length and a more realistic estimate of the asymptotes than Gompertz' curves. At fledging, the young had reached 95% of the mean mass of adults wintering in Africa, while bill and wing length still grow considerably after fledging (table 4.2). As growth may be similar among chicks within the same broods, the jack-knifed standard errors presented in table 4.2 could be underestimations. However, jack-knifing standard errors by serially excluding whole broods from the dataset instead of individual chicks produced similar results (e.g. for body mass: A=50.3 ± 1.2, K=0.33 ± 0.03, T=5.58 ± 0.27).

Daily mean air temperature reached maximum values (12-20°C) between 10 and 19 July. There was a distinct cold spell from 20 to 25 July, with mean temperatures of 2-5°C, strong winds, and rain and snowfall on several days. Ambient temperature affected growth rates of both body mass and bill length in young Curlew Sandpipers

TABLE 4.1. Percentage of Curlew Sandpiper broods observed in brood aggregations according to age of the chicks.

age (d)	N	% in aggregation
0–3	22	5%
4–6	16	50%
7–9	17	88%
10–12	11	73%
13–15	12	92%

FIGURE 4.3. Growth of body mass, bill length, tarsus length, and wing length in Curlew Sandpiper chicks. Black dots represent chicks of known age, and only these were used in fitting the growth curves. Open dots represent chicks of unknown hatch date that were captured twice, and in which the age at first capture was estimated by comparing their measurements to those of known-age chicks. Growth curve parameters are given in table 4.2.

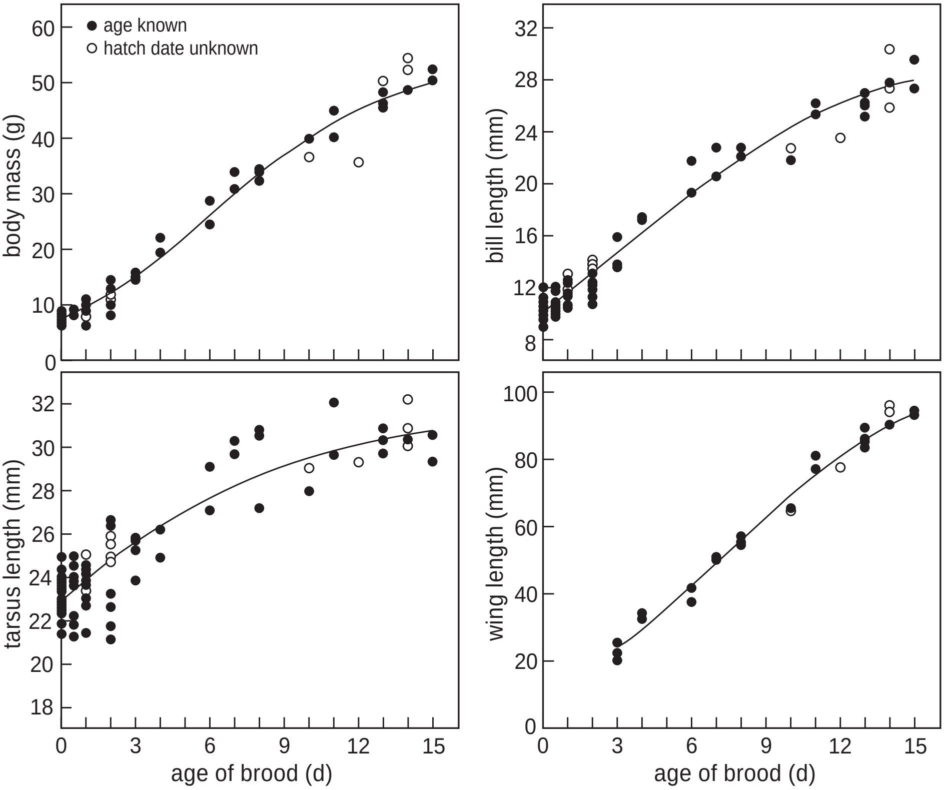


TABLE 4.2. Growth parameters for chicks of Curlew Sandpiper. The number of chicks contributing data (N), the three parameters of the logistic growth equation ($y(t)= A/[1+e^{-K(t-T)}]$) and their standard errors, and the size at hatching (Y$_h$), at fledging (Y$_f$), and when adult (Ad; Wymenga *et al.* 1990), are given.

variable	N	A	SE$_A$	K	SE$_K$	T	SE$_T$	Y$_h$	Y$_f$	Ad
body mass	29	52.09	1.54	0.314	0.020	5.89	0.32	8.2	49.6	52
bill length	50	30.12	1.25	0.205	0.018	3.15	0.53	10.8	27.8	38
tarsus	50	31.82	0.76	0.157	0.030	–6.02	0.80	23.2	30.8	31
wing	20	107.8	4.0	0.260	0.021	7.59	0.39	17	94.5	132

FIGURE 4.4. Growth rate indices (observed / expected growth) for body mass (A) and bill length (B) in relation to average temperature. Statistics in text.

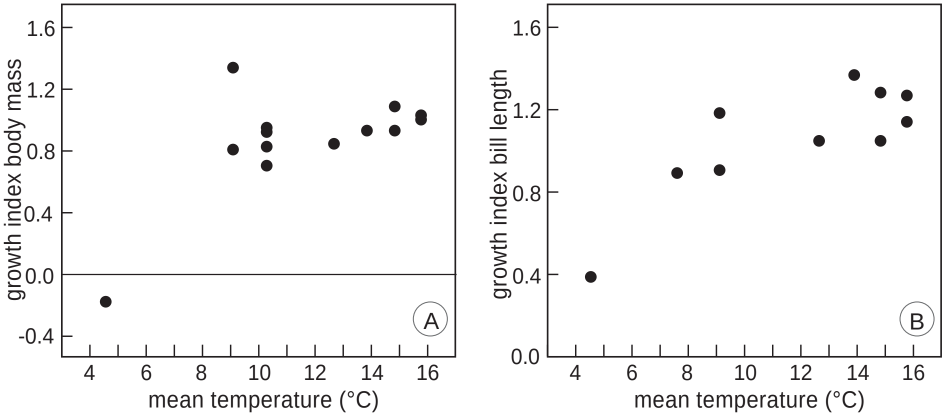
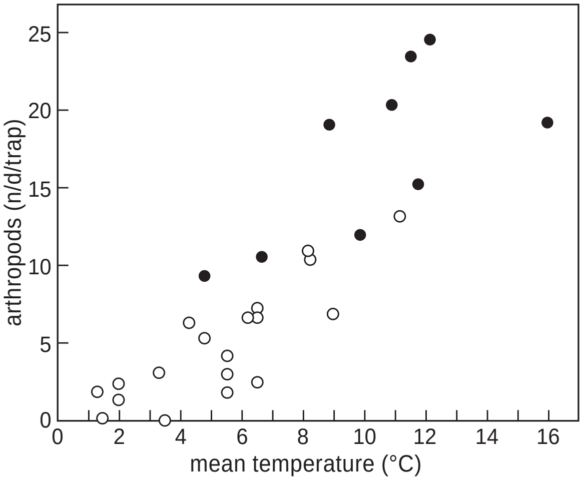


FIGURE 4.5. Relationship between mean daily temperature and the number of arthropods caught in pitfall traps (mites and springtails ≤1.5 mm excluded), 16 June - 6 August 1991. Black dots are data points from the period in which most chicks were present (10-31 July). Statistics in text.



(fig. 4.4). Although largely dependent on one datapoint, the relationship seemed curvilinear, with slower growth and even mass loss at the lowest temperature (regression equations derived by hierarchical linear modeling: mass, $y=-1.577+0.4053 \times -0.01544\ x^2$, $SE_{B1}=0.1058$, $t_9=3.83$, $P<0.01$, $SE_{B2}=0.00482$, $t_9=3.20$, $P<0.02$; bill, $y=-0.5896+0.2659 \times -0.00976\ x^2$, $SE_{B1}=0.0667$, $t_6=3.98$, $P<0.01$, $SE_{B2}=0.00309$, $t_6=3.16$, $P<0.02$). As the tarsus is largely fully grown in chicks of a week old, and very few pairs of measurements for wing length were available, no attempts were made to relate tarsus and wing growth to temperature.

The daily number of arthropods caught in the pitfall traps was closely related to mean temperature (fig. 4.5), both when viewed over the entire summer period (Poisson regression; $\log(y)=3.040+0.1755x$, change in deviance =1119.7, $P<0.001$) and in the period when most chicks were present (10-31 July, $\log(y)=4.408+0.069x$; change in deviance =68.5, $P<0.001$). On cold days, the availability of food for Curlew Sandpiper chicks, which foraged visually on surface-active prey, was thus markedly reduced.

Annual variation in breeding success

Because chick mortality was highest in the first week, weather effects on breeding productivity are most likely to be found shortly after the main hatching period, when many young chicks are present. In 1991, most Curlew Sandpiper chicks hatched between 10 and 15 July. Hatching dates elsewhere in Taimyr and in other years (table 4.3) show a similar phenology, with a tendency towards later dates in northern Taimyr and in years of late snow melt, notably 1992 and 1994. Hence, for the core breeding area which extends between 73°N and 75°N in Taimyr (Rogacheva 1992, Lappo 1996), it can

TABLE 4.3. Hatching phenology of Curlew Sandpipers on the Taimyr Peninsula. Hatching dates were observed directly or estimated from egg flotation, egg weights or chick biometrics. Sites are ordered according to latitude.

			hatching date				
site	coordinates		year	N	range	median	reference
Medusa Bay	73°20’N	80°30’E	1994	18		12.7	K. Günther & I. Hertzler unpubl.
Medusa Bay	73°20’N	80°30’E	1996	53	6.7 – 20.7	13.7	Tulp *et al.* 1997
Uboinaya River	73°37’N	82°20’E	1984	14	6.7 – 17.7	11.7	Tomkovich 1995
Pyasina Delta	74°08’N	86°45’E	1990	8	7.7 – 20.7	16.7	Hötker 1995
Pyasina Delta	74°08’N	86°45’E	1993	5	5.7 – 13.7	11.7	K. v. Dijk & P. Venema unpubl.
Pyasina Delta	74°08’N	86°45’E	1994	10	17.7 – 2.8	24.7	H. Vonk & A. Duiven unpubl.
Pyasina Delta	74°08’N	86°45’E	1995	12	10.7 – 24.7	13.7	J.L. Mulder unpubl.
Pronchishchev Lake	75°16’N	112°28’E	1991	30	10.7 – 26.7	12.7	this study
Pronchishchev Lake	75°16’N	112°28’E	1992	20	16.7 – 31.7	21.7	Spiekman & Groen 1993
Sterlegov Cape	75°26’N	89°08’E	1990	3	13.7 – 16.7	15.7	Hötker 1995
Sterlegov Cape	75°26’N	89°08’E	1994	5	16.7 – 4.8	24.7	Tulp *et al.* 1998
Knipovich Bay	76°05’N	98°32’E	1990	24	8.7 – 25.7	19.7	Tomkovich *et al.* 1994
Knipovich Bay	76°05’N	98°32’E	1991	19	30.6 – 30.7	17.7	Tomkovich *et al.* 1994
Knipovich Bay	76°05’N	98°32’E	1992	4	23.7 – 31.7	28.7	Tomkovich *et al.* 1994

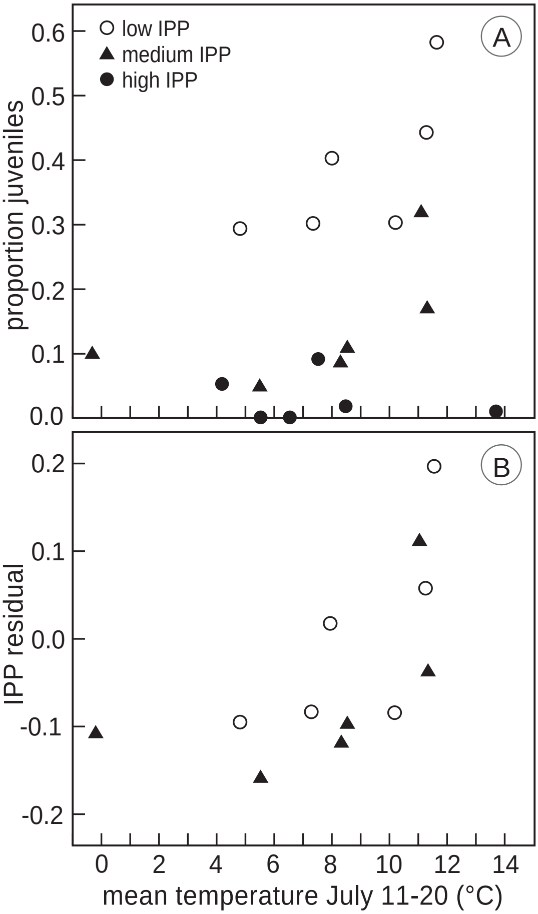


FIGURE 4.6. Relationship between mean temperature at the Pyasina river, Taimyr, between 10-20 July and the proportion of juvenile Curlew Sandpipers in winter catches in South Africa, divided into years with low, medium and high inferred predation pressure (IPP). A: untransformed data, B: residual productivities for years with medium and low IPP, after correcting for IPP effects. Statistics in table 4.4b.

be expected that if weather conditions affect chick survival, the second decade of July will be the critical period. Mean temperature in this period was therefore used as the primary weather variable to test for associations with variation in breeding productivity.

Summers & Underhill (1987) showed that Curlew Sandpiper breeding productivity during 1969-1986, measured in the wintering area, was significantly associated with lemming abundance and inferred predation pressure (IPP). They modelled IPP as a two-state variable, being either low (in years when lemming abundance is either the same or higher than in the previous year) or high (after a fall in lemming abundance). For 1977-1994 (the years for which weather data were available) as well, the effect of IPP proved highly significant (table 4.4a). Mean temperature during 11-20 July significantly improved the fit of the logistic regression model containing IPP (table 4.4a). There was also a significant interaction between IPP and temperature; in years of high IPP, the temperature effect was much weaker than in other years.

However, there are no *a priori* reasons for assuming predation levels to be the same in intermediate and peak lemming years, and the data suggested higher productivities in lemming peak years than in the preceding years (fig. 4.6a). When the category 'low IPP' was split into 'low' (in lemming peak years) and 'medium' (in the preceding years) for 1977-1994, the fit of the logistic regression model was significantly improved (table 4.4b), and the mean productivities for the low and medium IPP levels differed significantly from each other (t_{10}=2.66, P<0.05).

Adding mean temperature between 10 and 20 July to the regression model containing three levels of IPP again significantly improved its fit (table 4.4b). The temperature effect was absent in years of high IPP, while it was of similar magnitude in years of low and medium IPP (interaction temperature.3rd-level IPP n.s.; table 4.4b). Furthermore, the relationship between temperature and productivity was curvilinear, because the effect of temperature^2 was also significant. Breeding productivity was highest in years when average mid-July temperatures at the Pyasina River rose above 7-10°C (fig. 4.6b). IPP alone explained 77% of the total deviance in the data, and adding temperature effects increased this to 88%.

TABLE 4.4. Logistic regression models for the breeding productivity of Curlew Sandpipers, measured as the proportion of juveniles in ringing samples of birds wintering in South Africa (N=18 years). Explanatory variables tested were IPP (2 levels in (a), 3 levels in (b), mean temperature between 10 and 20 July and its square, and the interaction terms IPP x temperature and IPP x temperature^2. In model (b), IPP was entered first as a 2-level variable, after which a 3rd level was nested within the original level 2, to show the improvement of the fit associated with this 3rd level. The changes in deviance are cumulative; the regression coefficients are those for the final model including all significant terms (texts between brackets clarify when IPP terms apply).

		change in			estimates of		
	parameter	deviance	*df*	P	coefficient	SE	
(a)	constant				−2.91	2.17	
	IPP (2 levels)	185.20	1	<0.001	0.56	2.28	(IPP not high)
	temperature	39.62	1	<0.001	−0.087	0.292	
	IPP x temperature	7.60	1	<0.01	0.241	0.302	(IPP not high)
	residual	133.10	14				
	total	365.52	17				
(b)	constant				−1.74	1.54	
	IPP (2 levels)	185.20	1	<0.001	0.83	1.44	(IPP not high)
	IPP (3rd level)	95.87	1	<0.001	−1.31	0.304	(IPP medium)
	temperature	22.27	1	<0.001	−0.395	0.277	
	temperature x IPP (2 level)	6.08	1	<0.02	0.277	0.187	(IPP not high)
	temperature x IPP (3rd level)	0.01	1	>0.5			
	temperature^2	11.78	1	<0.01	0.018	0.012	
	residual	44.31	11				
	total	365.52	17				

For 14 years (1977-1990) for which mean wind speed during 11-20 July was available, this factor (and its interaction with IPP) increased the model fit even further than temperature did, to an explained deviance of 98%. However, in view of the small number of degrees of freedom left for the residual and the fact that the parameter estimates were biologically unbelievable and sensitive to the exclusion of some years from the data, this model is not presented here.

Mean temperature and wind speed during 11-20 July were not significantly different between years with low, medium or high IPP (ANOVA, temperature $F_{2,15}$=0.30, P=0.74; wind speed $F_{2,11}$=0.49, P=0.62). Hence, the correlations between breeding productivity and weather were not caused by an association between weather and the phase of the lemming cycle.

The selection of the second decade of July as the period to correlate breeding productivity and weather was made *a priori*, based on the sandpipers' breeding phenology. We also explored possible associations between productivity and weather in other periods of the birds' presence in the tundra, by calculating the correlation between the residual productivities after correcting for IPP (3 levels) with the date of snow melt and mean temperature, wind speed, and precipitation for each decade of June, July and August. Even without allowing for the fact that this involves multiple simultaneous comparisons, the correlations were not significant (P≥0.16) for 10-day periods other than the second decade of July.

DISCUSSION

Habitat choice and behaviour of families

The occurrence of brood aggregations in Curlew Sandpipers has been described by Haviland (1915) and Soloviev & Tomkovich (1992, 1998). Once arrived in the same area of preferred habitat, broods tended to stay relatively close together, and females cooperated in predator defence. Because Curlew Sandpiper females care for the eggs and young without help of the male (Portenko 1959, Holmes & Pitelka 1964, Tomkovich 1988) and stay with the brood until fledging, brood aggregations do not allow some of the adults to depart earlier, as was suggested for Bristle-thighed Curlews *Numenius tahitiensis* by Lanctot *et al.* (1995). Curlew Sandpipers may benefit from forming aggregations through shared vigilance and greater effectiveness of cooperative mobbing of predators. Soloviev & Tomkovich (1998) reported that Curlew Sandpipers were the most likely to occur in brood associations among five wader species present in their study area, and that they often joined other species that are more aggressive towards predators. In our study area, Turnstones sometimes served as such an 'umbrella species', but we did not observe associations with the even bolder Grey Plover *Pluvialis squatarola*, perhaps because these hatched *c.* 10 days later on average.

Movements of broods from nesting sites to rearing areas with a different (often wetter) vegetation type have been described for several arctic waders (Holmes 1966, Parmelee *et al.* 1968, Nettleship 1973, Flint & Kondratiev 1977, Ashkenazie & Safriel 1979, Miller 1983). Brood movements in precocial birds have been explained both as a means of locating good feeding sites (e.g. Erikstad 1985, Galbraith 1988), and to avoid attracting predators by continuous presence at one site. Under the predation hypothesis, daily brood movements should increase with age as the chicks become more valuable to the parent (Sonerud 1985). Contrary to this, brood movements in Curlew Sandpipers were largest in the first week of the chicks' life. In addition, families are more easily visible from a distance in the flat greenish marshes and sedge tundra than in the rugged brownish frost-heaved tundra. This suggests that in Curlew Sandpipers brood movements are not primarily an anti-predation adaptation, and that they are better explained by differences in food availability between nesting sites and chick-rearing areas. Hötker & Nehls (1995) and Tulp *et al.* (1997, 1998) found more arthropods in pitfalls and soil samples in moist grassy tundra and marshes than in dryer vegetations at three sites in NW Taimyr. Similarly at Barrow, Alaska, both adult insects and larvae were more common in July in lowland marshes, which were frequented most by Dunlin *Calidris alpina* broods, than in upland tundra (Holmes 1966).

Growth rate

Growth in Curlew Sandpiper chicks was rapid compared to that in other wader species. Beintema & Visser (1989a) described the allometric relationship between asymptotic mass (A, in g) and the Gompertz' growth coefficient in 15 species: $K_G = 0.390A^{-0.312}$. Conversion of the logistic rate parameter K_L to K_G (Ricklefs 1973) yields $K_G = 0.213$ for Curlew Sandpipers, 71% higher than the value (0.114) expected on the basis of this relationship. Apart from the fact that the allometric equation includes data on plovers (Charadriidae), which generally grow slower than sandpipers (Scolopacidae), the difference may be related to the high breeding latitude (Beintema & Visser 1989a). The short summer season here is likely to select for rapid growth.

Growth rate of Curlew Sandpiper chicks in our field study was reduced during cold weather. Several mechanisms may underlie this. Firstly, the time available for foraging for young chicks is reduced because they need increasing amounts of brooding when temperature decreases (Beintema & Visser 1989b, Visser & Ricklefs 1993a). Secondly, low temperatures and strong winds increase the chicks' energy expenditure for thermoregulation when not brooded by the parent. Thirdly, foraging success is likely to be reduced on cold days: we observed a strong decrease in surface activity of the arthropods on which the chicks feed. These mechanisms, singly or in combination, reduce the surplus of energy intake over expenditure that is necessary for growth.

Annual variation in breeding productivity

Although flyways between specific parts of the wintering and breeding ranges are not well separated in the Curlew Sandpiper, and birds wintering in South Africa may breed on Taimyr as well as further east (Underhill 1995), birds breeding in eastern Siberia are more likely to winter in southern Asia and Australia than in Africa. Thus, many of the Curlew Sandpipers wintering in South Africa probably originate from the large Taimyr population, and factors affecting their breeding success may be looked for in that area.

The weather station at the Pyasina delta is situated within the core of the Curlew Sandpiper's main breeding range on Taimyr (Lappo 1996). Although Pronchishchev Lake is situated *c.* 770 km to the NE on the opposite side of the peninsula, daily mean temperatures at the two sites were significantly correlated in late June-early August

1991 (r_{51}=0.55, P<0.001). A stronger correlation existed between mean temperature at the Pyasina Delta and at Pronchishchev Lake two days later (r_{51}=0.74, P<0.001), reflecting the generally eastward progression of weather systems across the peninsula. Therefore, the Pyasina weather data are representative of general conditions across a major part of Taimyr.

Breeding productivity is composed of four sequential components: the proportion of females in the population producing a clutch, clutch size, clutch survival and chick survival. Clutch size variation is small in Curlew Sandpipers, as it is in arctic-breeding waders in general (Maclean 1972), and is therefore not expected to have a significant effect on breeding productivity. No data exist for Curlew Sandpipers on the size of any non-breeding segment of the adult population. The lack of a correlation between June weather and breeding productivity found in this study suggests that variation in this segment may not be substantial, or is independent of weather. Curlew Sandpipers show no breeding site fidelity (Underhill *et al*. 1993, Tomkovich & Soloviev 1994), and numbers in the southern part of the breeding range tend to increase in years of late snow melt (Haviland 1915, Hötker 1995, Lappo 1996), suggesting that females may avoid non-breeding years by settling in areas with better snow conditions.

Although there is variation in the viability of eggs, which may be weather-related (Tomkovich 1995), the main factor affecting hatching success is predation. This is indicated by the strong association between breeding productivity and lemming abundance (Summers & Underhill 1987, this study), and by the field observations at Pronchishchev Lake during the lemming peak of 1991, when all observed clutches hatched, and the following lemming low year, when only 1% of wader clutches, including Curlew Sandpipers', survived predation by Arctic Foxes and skuas (Underhill *et al*. 1993).

Chicks may become victims of predation too, but their survival is also affected by weather conditions and food availability. Cold weather increases the risk that chicks die of exposure, and was shown in this study to reduce growth rate (see also Chapter 3). This may lead to postponed fledging and prolonged exposure to predation. When adverse conditions prevail for more than a few days, they may result in starvation, as arctic wader chicks do not carry substantial fat reserves that can be invoked to overcome such periods (Norton 1973). Indeed, weather conditions in Taimyr during the main chick period explained a substantial part of the remaining variation in breeding productivity after inferred predation pressure had been accounted for. Given that the three defined levels of IPP and the proportion of juveniles in the South African winter catches are imperfect estimators of hatching success and breeding productivity respectively, the effects of weather on chick survival must be large and operate over an extensive geographical area to show up so clearly.

There have been few earlier attempts to relate breeding productivity of arctic-breeding waders to summer weather conditions, though Evans & Pienkowski (1984) proposed that 'the major factor affecting reproductive output would appear to be weather at high latitudes'. Boyd (1992) showed that changes in wintering numbers of Knots *Calidris canutus* in Britain were correlated with June temperatures in their Nearctic breeding range, but found no association between June temperatures, or other measures of summer weather, and the proportion or number of juveniles in the wintering population.

Effects of early breeding season weather on productivity have been demonstrated in several arctic-breeding geese (Boyd 1965, 1987, Kostin & Mooij 1995, Sheaffer & Malecki 1996, Skinner *et al*. 1998). Spring phenology affects the timing of laying and/or the female's energy budget during the prelaying period, which in combination determine clutch size, including the decision whether to breed at all (Uspenski 1965, Davies & Cooke 1983, Ganter & Cooke 1996). In contrast, Curlew Sandpiper productivity was correlated with conditions in the fledging period, but not with early spring weather. Wader chicks are less homeothermic than young waterfowl (Visser & Ricklefs 1993b), which renders the time that they can spend foraging instead of being brooded more sensitive to temperature. In addition, the food supply of insectivorous wader chicks is more sensitive to short-term variation in weather conditions than that of geese which take more plant material. Gardarsson & Einarsson (1997) did find productivity effects of weather and food availability during the fledging period in Wigeon *Anas penelope*, the chicks of which feed mainly on chironomids. Boyd (1996) reported correlations between the number of first-winter Long-tailed Ducks *Clangula hyemalis* shot in eastern North America and both summer and autumn temperatures in their breeding range. Since most goose studies have considered weather effects during the early part of the breeding season only, the suggestion that breeding productivity of arctic geese is more sensitive to conditions in the arctic spring, while waders are more affected by mid-summer weather, remains open for testing.

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REFERENCES

- Ashkenazie S. & U.N. Safriel 1979. Breeding cycle and behaviour of the Semipalmated Sandpiper at Barrow, Alaska. Auk 96: 56-57.
- Beintema A.J. & G.H. Visser 1989a. Growth parameters in chicks of charadriiform birds. Ardea 77: 169-180.
- Beintema A.J. & G.H. Visser 1989b. The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77: 181-192.
- Boyd H. 1965. Breeding success of White-fronted Geese from the Nenets National Area. Wildfowl Trust Annual Report 16: 34-40.
- Boyd H. 1987. Do June temperatures affect the breeding success of Dark-bellied Brent Geese *Branta b. bernicla*? Bird Study 34: 155-159.
- Boyd H. 1992. Arctic summer conditions and British Knot numbers: an exploratory analysis. Wader Study Group Bulletin 64, Suppl.: 144-152.
- Boyd H. 1996. Arctic temperatures and the Long-tailed Ducks shot in eastern North America. Wildlife Biology 2: 113-117.
- Byrk A.S. & S.W. Raudenbush 1992. Hierarchical linear models, application and data analysis. Sage, London.
- Chernov. Yu.I. 1985. The living tundra. Cambridge University Press, Cambridge.
- Davies J.C. & F. Cooke 1983. Annual nesting productivity in Snow Geese: prairie drought and arctic springs. Journal of Wildlife Management 47: 291-296.
- Dhont A.A. 1987. Cycles of lemmings and geese: a comment on the hypothesis of Roselaar and Summers. Bird Study 34: 151-154.
- Ebbinge B.S. 1989. A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla*. Ibis 131: 196-204.
- Ebbinge B.S. 1990. Reply by Barwolt S. Ebbinge. Ibis 132: 481-482.
- Erikstad K.E. 1985. Growth and survival of Willow Grouse chicks in relation to home range size, brood movements and habitat selection. Ornis Scandinavica 16: 181-190.
- Evans P.R. & M.W. Pienkowski 1984. Population dynamics of shorebirds. In J. Burger & B.L. Olla (eds). Shorebirds - breeding behavior and populations: 83-123. Behavior of marine animals. Vol. 5. Plenum, New York.
- Flint V.E. & A.J. Kondratiev 1977. Materialien zur Biologie des Kiebitzregenpfeifers (*Pluvialis squatarola* L.). Beitrage zur Vogelkunde 23: 265-277.
- Galbraith H. 1988. Effects of agriculture on the breeding ecology of Lapwings *Vanellus vanellus*. Journal of applied Ecology 25: 487-503.
- Ganter B. & F. Cooke 1996. Pre-incubation feeding activities and energy budgets of Snow Geese: can food on the breeding grounds influence fecundity? Oecologia 106: 153-165.
- Gardarsson A. & A. Einarsson 1997. Numbers and production of Eurasian Wigeon in relation to conditions in a breeding area, Lake Myvatn, Iceland. Journal of Animal Ecology 66: 439-451.
- Genstat 5 Committee 1993. Genstat 5 release 3 reference manual. Oxford Science Publications, Oxford.
- Haviland M. 1915. Notes on the breeding biology of the Curlew Sandpiper. British Birds 7: 178-183.

- Hayman P., J. Marchant & T. Prater 1986. Shorebirds. Croom Helm, London.
- Holmes R.T. 1966. Feeding ecology of the Red-backed Sandpiper *(Calidris alpina)* in arctic Alaska. Ecology 47: 32-45.
- Holmes R.T. & F.A. Pitelka 1964. Breeding behaviour and taxonomic relationships of the Curlew Sandpiper. Auk 81: 362-379.
- Hötker H. 1995. Avifaunistical records of the WWF expeditions to Taimyr in the years 1989, 1990 and 1991. In P. Prokosch & H. Hötker (eds), Faunistik und Naturschutz auf Taimyr: 34-89. Corax 16, Sonderheft.
- Hötker H. & G. Nehls 1995. Evertebraten als Nahrungsgrundlage für Vögel in Nordwest-Taimyr im Juni und Juli 1990. In P. Prokosch & H. Hötker (eds), Faunistik und Naturschutz auf Taimyr: 25-33. Corax 16, Sonderheft.
- Institute of Education 1995. MLN software for multilevel-analysis, V10a. Institute of Education, University of London, London.
- Kostin I. & J.H. Mooij 1995. Influence of weather conditions and other factors on the reproductive cycle of Red-breasted Geese *Branta ruficollis* on the Taimyr Peninsula. Wildfowl 46: 45-54.
- Lanctot R.B., R.E. Gill Jr., T.L. Tibbets & C.M. Handel 1995. Brood amalgamation in the Bristle-thighed Curlew *Numenius tahitiensis*: process and function. Ibis 137: 559-569.
- Lappo E.G. 1996. Comparisons of breeding range structure for Dunlin *Calidris alpina* and Curlew Sandpiper *Calidris ferruginea*: conservative and nomadic tundra waders. Wader Study Group Bulletin 80: 41-46.
- Maclean G.L.. 1972. Clutch size and evolution in the Charadrii. Auk 89: 299-324.
- Miller E.H. 1983. Habitat and breeding cycle of the Least Sandpiper *Calidris minutilla* on Sable Island, Nova Scotia. Canadian Journal of Zoology 61: 2880-2898.
- Nettleship D.N. 1973. Breeding ecology of Turnstones *Arenaria interpres* at Hazen Camp, Ellesmere Island, N.W.T. Ibis 115: 202-217.
- Norton D.W. 1973. Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph.D Dissertation, University of Alaska, Fairbanks.
- Parmelee D.F., D.W. Greiner & W.D. Graul 1968. Summer schedule and breeding biology of the White-rumped Sandpiper in the central Canadian arctic. Wilson Bulletin 80: 5-29.
- Portenko L.A. 1959. Studien an einigen seltenen Limicolen aus den nordlichen und ostlichen Sibirien II - Der Sichelstrandlaufer *Erolia ferruginea* (Pontopp.). Journal für Ornithologie 100: 141-172.
- Ricklefs R.E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115: 177-201.
- Rogacheva, H. 1992. The birds of central Siberia. Husum Drück- und Verlagsgesellschaft, Husum.
- Roselaar C.S. 1979. Fluctuaties in aantallen Krombekstrandlopers *Calidris ferruginea.* Watervogels 4: 202-210.
- Ryabitsev V.K. 1993. Breeding conditions for waders in the tundras of Russia in 1991. Wader Study Group Bulletin 71: 20-25.
- Schekkerman H. & M. van Roomen (1995) Breeding waders at Pronchishcheva Lake, northeastern Taimyr, Siberia, in 1991. WIWO report 55. WIWO, Zeist.
- Schoener T.W. & A. Schoener 1978. Estimating and interpreting body-size growth in *Anolis* lizards. Copeia 1978(3): 390-405.

- Sheaffer S.E. & R.A. Malecki 1996. Predicting breeding success of Atlantic population Canada Geese from meteorological variables. Journal of Wildlife Management 60: 882-890.
- Skinner W.R., R.L. Jefferies, T.J. Carleton, R.F. Rockwell & K.F. Abraham 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. Global Change Biology 4: 3-16.
- Sokal R.R. & F.J. Rohlf 1981. Biometry. Freeman, San Francisco.
- Soloviev M.Yu. & P.S. Tomkovich 1992. Brood aggregations in waders at northern Taimyr. Wader Study Group Bulletin 65: 18.
- Soloviev M.Yu. & P.S. Tomkovich 1998. The phenomenon of brood aggregations in waders (Charadrii) and their structure in northern Taimyr. International Wader Studies 10: 201-206.
- Sonerud G.A. 1985. Brood movements in grouse and waders as defence against win-stay search in their predators. Oikos 44: 287-300.
- Spiekman H. & N. Groen 1993. Breeding performance of arctic waders in relation to lemming densities, North-East Taimyr, Siberia, 1992. WIWO report 33. WIWO, Zeist.
- Stanley P.I. & C.D.T. Minton 1972. The unprecedented westward migration of Curlew Sandpipers in autumn 1969. British Birds 65: 365-380.
- Summers R.W. 1986. Breeding production of Dark-bellied Brent Geese in relation to lemming cycles. Bird Study 33: 105-108.
- Summers R.W. & L.G. Underhill 1987. Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. Bird Study 34: 161-171.
- Tomkovich P.S. 1988. Mating system and parental care in the Curlew Sandpiper. Studies and protection of birds in Northern ecosystems. USSR Academy of Sciences, Vladiwostok: 185-188.
- Tomkovich P.S. 1994a. Breeding conditions for waders in Russian tundras in 1992. Wader Study Group Bulletin 75: 20-26.
- Tomkovich P.S. 1994b. Breeding conditions for waders in Russian tundras in 1993. Wader Study Group Bulletin 75: 27-34.
- Tomkovich P.S. 1995. Does the wind influence egg fertility? A probable case with Curlew Sandpiper *Calidris ferruginea*. Wader Study Group Bulletin 77: 48-49.
- Tomkovich P.S. & M.Yu. Soloviev 1994. Site fidelity in high arctic breeding waders. Ostrich 65: 174-180.
- Tomkovich P.S., M.Yu. Soloviev & E.E. Syroechkovski Jr. 1994. Birds of arctic tundras of northern Taimyr (Knipovich Bay region). In E.V. Rogacheva (ed.), Arctic tundras of Taimyr and Kara Sea Islands: nature, fauna and conservation problems. Nauka, Moscow.
- Tulp I., L. Bruinzeel, J. Jukema & O. Stepanova 1997. Breeding of waders at Medusa Bay, NW Taimyr, in 1996. WIWO report 57. WIWO, Zeist.
- Tulp I., H. Schekkerman, T. Piersma, J.Jukema, P. de Goeij & J. van de Kam 1998. Breeding waders at Cape Sterlegova, NW Taimyr, in 1996. WIWO report 61. WIWO, Zeist.
- Underhill L.G. 1990. Breeding productivity of Siberian Knots and Curlew Sandpipers, 1987-1989. Safring News 19: 3-6.
- Underhill L.G. 1995. The relationships between breeding and nonbreeding localities of waders: the Curlew Sandpiper *Calidris ferruginea* as an extreme example. Ostrich 66: 41-45.
- Underhill L.G. & T.B. Oatley, 1995. Breeding productivity of Curlew Sandpipers, 1990-1994. Safring News 24: 77-78.

- Underhill L.G., R.P. Prys-Jones, E.E. Syroechkovski, Jr., N.M. Groen, V. Karpov, M.W.J. van Roomen, A. Rybkin, H. Schekkerman, H. Spiekman & R.W. Summers 1993. Breeding of waders (Charadrii) and Brent Geese *Branta bernicla benicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. Ibis 135: 277-292.
- Underhill L.G., M. Waltner & R.W. Summers 1989. Three-year cycles in breeding productivity of Knots *Calidris canutus* wintering in South Africa suggest Taimyr provenance. Bird Study 36: 83-87.
- Uspenski S.M. 1965. The geese of Wrangel Island. Wildfowl Trust Annual Report 16: 126-129.
- Visser G.H. & R.E. Ricklefs 1993a. Development of temperature regulation in shorebirds. Physiological Zoology 66: 771-792.
- Visser G.H. & R.E. Ricklefs 1993b. Temperature regulation in neonates of shorebirds. Auk 110: 445-457.
- Wymenga E., M. Engelmoer, C.J. Smit & T.M. van Spanje 1990. Geographical origin and migration of waders wintering in West Africa. Ardea 78: 83-112.
- Yurlov A.K. 1993. Breeding conditions for waders in the tundras of the USSR in 1990. Wader Study Group Bulletin 67: 57-62.

Foraging in precocial chicks of the Black-tailed Godwit *Limosa limosa*: sensitivity to weather and prey size

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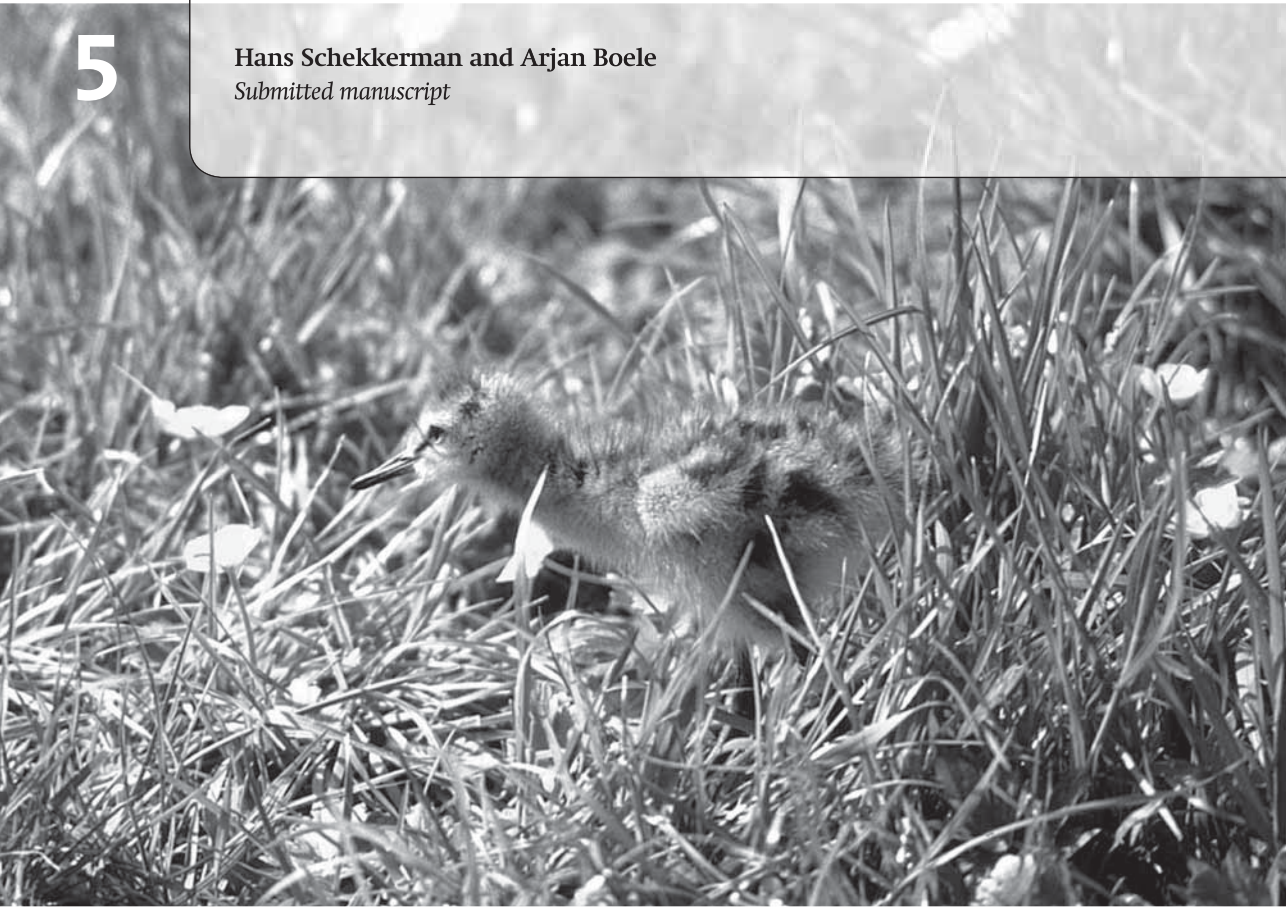
Submitted manuscript



1. Self-feeding precocial birds hatch with highly developed functional capabilities, yet still undergo significant ontogenic change before fledging. This mode of development results in high energy requirements and renders chicks sensitive to foraging conditions. We studied development of foraging behaviour during the 25-day prefledging period in the insectivorous chicks of the declining, grassland-breeding Black-tailed Godwit *Limosa limosa*.

2. Until 8-10 days old, parental brooding was the main determinant of chicks' daily foraging time. Brooding decreased with age and temperature, and increased during rainfall. Foraging time increased to 70-90% of the daylight period in chicks older than a week, during which distances of 3-12 km/day were covered.

3. Chicks took 98% of their arthropod prey from the grassland vegetation. Prey ingestion rates increased in the first week of life and slowly declined thereafter, modified by wind speed (negative effect), temperature and time of day.

4. Chicks in poor body condition were brooded more than chicks growing normally and hence had less feeding time, potentially leading to a negative condition spiral under adverse conditions. We found no effect of condition on prey ingestion rate that would preclude recovery when conditions improve.

5. Combining behavioural observations with data on energy expenditure revealed that mean prey size was small (1-4.5 mg), necessitating a high feeding rate, but increased notably after 7-10 days. This coincided with a decrease in walking speed, suggesting that chicks fed more selectively.

6. Prey of older chicks approached the upper limit of sizes available in exploitable densities in the vegetation. In modern agricultural grasslands fewer large prey may be present than in the godwits' original breeding habitats, and this may enhance the sensitivity of chicks to variation in prey availability caused by weather and agricultural practice.

INTRODUCTION

The offspring of the great majority of bird species are fed by their parents or other adults for most or all of the prefledging period. In many such altricial and semiprecocial birds (Nice 1962), foraging behaviour develops gradually after fledging, while the young still receive additional food from adults for a shorter (Davies 1976, Moreno 1984, Wheelwright & Templeton 2003) or longer period (Heinsohn 1991, Langen 1996, Safriel *et al.* 1996). In some avian taxa however (particularly Struthiformes, Galliformes, Anseriformes, and most shorebirds Charadrii), the young feed for themselves from hatching onwards (Starck & Ricklefs 1998). This means that after the first few days, during chicks can sustain themselves on internal energy stores including the yolk sac, foraging abilities must have developed sufficiently to secure their daily food requirements. Precocial chicks hatch in a highly developed state relative to parent-fed altricials, with respect to thermoregulation and locomotion (Starck 1998, Visser & Hohtola 1998) but also sensory and cognitive features (Bennet & Harvey 1985, Nol 1986).

While self-feeding frees the parents from the demanding task of securing and transporting food, this burden is shifted to the chick. High energy requirements associated with foraging outside the nest (Schekkerman & Visser 2001) combined with a still incomplete development are likely to render precocial chicks sensitive to foraging conditions. Failure to achieve a positive energy balance precludes growth and ultimately results in starvation. If a reduced body condition in turn affects the chick's foraging performance, this may lead to a negative spiral precluding recovery when temporarily adverse foraging conditions improve. Such a scenario is less likely for parent-fed birds, although sibling competition might induce similar effects in some brood members. Weather may be one cause of such adverse conditions, by restricting foraging time of chicks that are not yet fully homeothermic (Beintema & Visser 1989b, Visser & Ricklefs 1993) or by reducing food availability. Man-made changes to foraging habitats may also reduce prey abundance.

In comparison to that of parent-fed species, the development of foraging behaviour has rarely been studied in self-feeding precocial chicks in the wild (but see Pienkowski 1984a, 1984b). Here, we describe the development of time budgets, foraging behaviour and prey size between hatching and fledging in the Black-tailed Godwit *Limosa limosa*, a shorebird breeding in wet grasslands. While adult godwits feed primarily on buried earthworms and Tipulid larvae during the breeding season, their chicks are mainly insectivorous. The European population, nowadays mainly confined to agricultural habitats, has been negatively affected by agricultural intensification, and a reduction in chick survival has been identified as a major driver of this decline (Thorup 2006, Chapter 7). In particular, advancement of mowing dates, increased fertilisation and widespread reseeding of grassland have increased mowing mortality, made chicks more vulnerable to predation, and reduced availability of arthropod prey (Schekkerman & Beintema 2007, Chapter 8). In view of these food availability problems, we investigated how food intake of godwit chicks depends on environmental conditions and on their own body condition, and explore the role of prey size in the chicks' feeding ecology.

METHODS

Study area and observational setup

Observations of Black-tailed Godwits were made in 1992-1995 in lowland wet grasslands near Baarn in The Netherlands (52°12'N, 15°19'E). The study area was a meadowbird reserve with a high water table (ditch level *c.* 0.3 m below field level in spring), moderate fertiliser input (100 kg N/ha /yr as farmyard manure), and a single hay cut in mid-June followed by low-intensity grazing in summer and autumn. This grassland type is a preferred habitat of Black-tailed Godwit broods (Schekkerman & Beintema 2007).

To allow close observation of godwit broods, enclosures that kept chicks inside but allowed the parents to freely move in and out were built around nests during the later stage of incubation. Enclosures measured 0.2 (1992 and 1993), 0.4 (1994) and 0.6 ha (1995). Fences were made of 50 cm high wire fencing (10 mm mesh), with black plastic cloth attached to the lower 25 cm to prevent adults from attempting to brood chicks through the fence. No additional food was offered besides the arthropods occurring naturally in the vegetation and soil. Water for drinking and bathing was present in footdrains or in dug-in trays. Behavioural observations were made from a hide placed on 1.5 m high scaffolding directly beside the enclosure.

Chicks were made individually identifiable at hatching by coloured leg rings. They were recaptured at intervals to record measurements and weight and to measure energy expenditure. Chicks were usually captured on two successive days and then left in peace for 2-3 days. Fifteen measurements of Daily Energy Expenditure (DEE) were made on enclosed chicks with the doubly labelled water method, and chick energy budgets were derived from these (Schekkerman & Visser 2001, Chapter 2). As shorebird chicks do not carry substantial fat deposits that can be used to overcome periods of food shortage (Schekkerman & Visser 2001), variations in energy balance will directly affect their growth rate. Condition of chicks was therefore described by dividing their body mass by the average mass of free-living Dutch godwit chicks of the same age (from Beintema & Visser 1989a). Indices were interpolated linearly for days when chicks were not measured. Condition indices ranged between 0.44 and 1.15 (mean 0.81, SD=0.12, N=127 chick-days).

Time budgets

Except in 1992 when few observations were made after 14:00, behavioural observations usually covered entire daylight periods (*c.* 6:00-22:00) in 2-3 observer shifts. A continuous record (resolution 1 minute) was kept of the time budgets of chicks and adults. Activities recognised in chicks were: being brooded by a parent, foraging, inactivity (sleep, bathing, preening and hiding upon alarm), walking along the fence (in response to a parent calling chicks from outside the enclosure), and 'out of view'. As it was common for chicks foraging in the rear of the enclosure to be hidden from view by vegetation for substantial periods, particularly later in the spring, we assumed that foraging chicks that were out of view for <10 minutes continued foraging in the meantime. Brooding bouts were not missed, since their occurrence was clear from parental behaviour and from the cessation of contact calls when all chicks had assembled beneath a parent.

As a rule, all chicks joined and ended bouts of brooding within the same minute, and broods were treated as behaving synchronously. Only when one or two chicks joined or left more than a minute earlier or later than their siblings or skipped a brooding bout altogether, separate recordings were made for these chicks.

For analysis, total observation time and time spent on each behaviour were summed per clock-hour (e.g. 6:00-7:00). Time budgets were summarised into 'brooding time' and 'potential foraging time', the latter including all activities other than brooding. Time spent walking along the fence was included in potential foraging time as we presume that fence walking did not occur at the expense of brooding. Hours with ≥20 observation minutes were used for analysis. In addition to 479 h of observations at Baarn, 499 h of observations made in 1981 and 1984 at the Kievitslanden, 20 km to the NE, were included to increase the range of age/weather combinations (Beintema & Visser 1989b, original data made available by A.J. Beintema and G.H. Visser). Methods here were identical to those at Baarn, but observations distinguished only time spent brooding and non-brooding.

Foraging behaviour

Whenever foraging chicks came close enough to the hide, foraging success was recorded. A focal chick was selected and observed for *c*. 1 minute, during which the number of prey items swallowed was counted. The duration of each observation was timed with a chronometer, stopped and restarted when a chick momentarily disappeared behind vegetation. If the chick remained out of view for more than 15 s, the observation was aborted. Recordings lasting 30 s or more were used for analysis. After each recording, a different chick was selected if available and a new one was started. Most prey taken by chicks were too small to be identified, but the swallowing movements of head and bill were usually well visible. Aborted and apparently unsuccessful pecks (which formed a small fraction) were not counted. For each prey the height at which it was captured was recorded as 'high' (from vegetation above the walking chick's head level), 'low' (from vegetation at or below head level), or 'ground' (taken from the ground).

Foraging observations were made by a total of nine observers, but the 1st author made 47% of all scans. New observers made one or two 4-6 hour training sessions with experienced ones to standardise methods and interpretation of behaviour, and observer differences were taken into account in data analysis.

In 1994 and 1995, we also recorded the number of steps made by chicks per minute of foraging, during separate scans mixed between feeding success observations. Pace lengths at different ages were measured in five chicks that were hand-raised to experimentally compare feeding success in differently managed grasslands (Schekkerman & Beintema 2007). Number of paces made when walking 6 m through 10-15 cm high grass was counted and averaged over three runs. Since the captive chicks grew somewhat faster than wild ones, the relationship between pace length and tarsus length of the captive chicks, rather than their age, was used to convert pace rates (steps/s) of wild chicks to walking speed (m/s).

Prey size

Most prey taken by chicks were too small to record their identity or size in the field. We estimated the average size of ingested prey by combining results of foraging observations, time-activity budgets, and data on chick energy requirements (from Schekkerman & Visser 2001), based on the premise that energy intake should equal expenditure (including growth) on a daily basis. Mean size of ingested prey at each age a (M_a, mg dry mass) was calculated as:

$$M_a = (1000 \times R_a) / (60 \times F_a \times I_a \times E \times Q),$$

where
R_a = Chick energy requirements (Metabolised Energy ME, kJ/day), calculated from body mass and growth rate using equations in Schekkerman & Visser (2001). We took into account that newborn chicks derive part of their energy requirements from the yolk sac by subtracting its energy content (33.5 kJ, Visser & Ricklefs 1995) from ME divided equally over three days,
F_a = time spent foraging (h/day),
I_a = average observed prey ingestion rate (n/min) of foraging chicks,
E = average energy density of arthropod prey (23 kJ/g dry mass, Cummins & Wuycheck 1971, Robel *et al.* 1995), and
Q = digestibility of prey (energy assimilated/energy ingested), assumed to be 0.74 (Castro *et al.* 1989). Digestibility of food pellets to captive-reared godwit chicks was independent of chick age (Schekkerman & Visser 2001, Chapter 2).

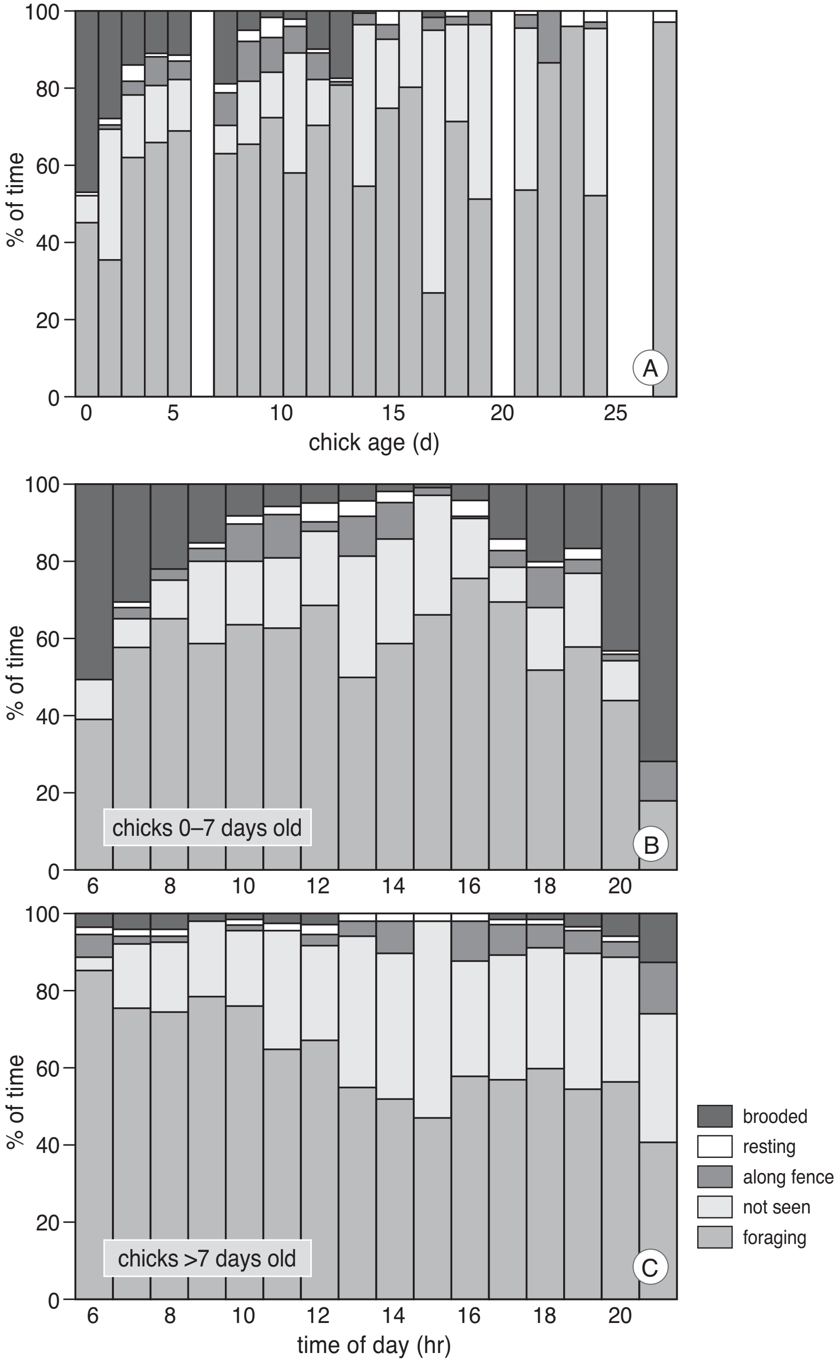
Minimum and maximum estimates of foraging time were derived from the time budget observations as, respectively, the time that chicks were seen foraging, and daylight time (16 hours) minus time recorded as spent on behaviour other than foraging and 'out of view'. As foraging time is the largest source of uncertainty in these estimations, we calculated minimum and maximum estimates of M_a using minimum and maximum foraging time, ignoring uncertainty in other parameters.

Environmental variables

Weather conditions were automatically recorded in the study area every two minutes. Wind speed was measured with a calibrated anemometer at 3 m above the ground. We recorded temperature (T_{bs}) of a blackened copper sphere (∅ 4 cm) placed in the vegetation at 10 cm above the ground to obtain a measure that integrates the effects of air temperature and solar radiation, and approximates the thermal environment experienced by chicks better than air temperature (measured in the shade at 1.5 m height) alone (Walsberg & Weathers 1986). Air temperature recorded at Kievitslanden (at 10 cm height) was converted to T_{bs} using linear regression and temperature and global radiation data from the national weather centre at 10-25 km from the study sites as an intermediary (all R^2>0.90). Occurrence and duration of rainfall were recorded during observations.

Abundance of vegetation-dwelling invertebrates was sampled weekly between 30 april and 18 June in five photo-eclectors (base area 0.25 m^2) in four fields that either

FIGURE 5.1. Time budgets of Black-tailed godwit chicks in relation to age (A) and time of day (B,C). Data obtained at Baarn; N=1016 observation bouts totalling 479 hours on 40 different days in 1992-95, and involving 8 broods in 4 different enclosures.



included the enclosure or lay nearby and had the same management history (see Schekkerman & Beintema 2007 for details). Trapped invertebrates were counted and their body length measured to the nearest 0.5 mm in animals ≤5 mm and to 1 mm in larger ones. Lengths were converted to dry mass using equations given in Rogers *et al.* (1976, 1977) or derived by drying and weighing own material. The overall relationship for arthropods in our samples was: mass (mg) = 0.3 length $(\text{mm})^{2.4}$ (Schekkerman 1997). Because larger arthropods make more profitable prey and may therefore be selected by godwit chicks, we used both total density (excluding the tiny Acarina and non-sminthurid Collembola), and density of arthropods with an individual dry mass >1 mg as measures of arthropod abundance during chick foraging observations. The complete sampling data were also used to construct the size-density distribution of arthropods on offer in the grassland vegetation. For comparison, we also constructed this distribution for four nearby fields used for intensive dairy farming (see Schekkerman & Beintema 2007).

Statistical analysis

To explore effects of chick age, condition and weather on the fraction of time spent brooded, we used a Generalized Linear Mixed Model (GLMM) with binomial distribution and logit link, estimating a dispersion parameter from the data to allow for over- or underdispersion. Brood and date nested within brood were included as random terms. Variables tested as fixed terms were chick age, condition index, T_{bs}, wind speed, and presence or absence of rainfall. Wald tests were used to assess significance of terms (at $P<0.05$). To analyse effects of age and environmental conditions on the number of prey ingested per minute foraging we used a GLMM with Poisson distribution and logarithmic link. The random model included brood, chick nested within brood, week nested within chick, day nested within week, and observer, to account for observer effects, dependencies between observations on the same broods and chicks, and the fact that some independent variables were measured per week (arthropod abundance) and others per day (age, condition) or per observation (time, wind, T_{bs}). We started the analysis with a full model including all variables (plus squared terms to account for non-linear effects) and first-order interactions between age and other variables, and then dropped first interactions, then squared terms, and then other terms until all variables in the model were significant. Finally we tested whether condition index and two measures of arthropod density improved the reduced models.

RESULTS

Time budgets

Godwit chicks were brooded by a parent for parts of the daylight period until about 8-10 days old (fig. 5.1). Chicks were brooded particularly in the morning and evening, and probably throughout the night; this was suggested by the fact that brooding sessions often extended for long uninterrupted periods until observers left the hide around nightfall, and that in the early morning broods were often located at the same spot where they were left the evening before. Older chicks were only brooded at daytime during rain, but were still brooded after dusk up to an unknown age. The remaining daylight time was mainly devoted to foraging. Young chicks sometimes spent substantial time walking along the fence in response to a parent trying to lead them away from the enclosure, but older chicks usually quickly resumed foraging. Chicks were out of view for considerable periods, especially later in the spring when the vegetation was high. Judging from behaviour on days when they were almost continuously visible (fig. 5.1a), most of the 'out of view' time was spent foraging, but

TABLE 5.1. GLMM (fixed part) for the fraction of time spent brooded in relation to chick age, weather variables and condition of godwit chicks (N=1016 observation bouts totalling 993 hours on 70 different days in 6 years, and involving 15 broods in 6 different enclosures). Presented are the reduced model resulting from backward elimination of insignificant terms (with regression coefficients B on the logit scale) and tests for effects of adding windspeed and interactions with age to the reduced model.

Fixed term	Wald statistic	d.f.	P	B	se(B)
Constant				5.73	1.04
Age of chicks (d)	93.84	1	<0.001	−0.5753	0.0662
Temperature (T_{bs}, °C)	329.30	1	<0.001	−0.1933	0.0224
Rain (0 or 1)	58.89	1	<0.001	0.374	0.395
Age x Rain	6.95	1	0.008	0.1760	0.0868
Condition Index	6.58	1	0.010	−2.400	0.960
+Wind speed (m/s)	0.27	1	0.61		
+Age x T_{bs}	0.05	1	0.82		
+Age x Condition	2.38	1	0.12		
+Age x Wind speed	0.97	1	0.32		

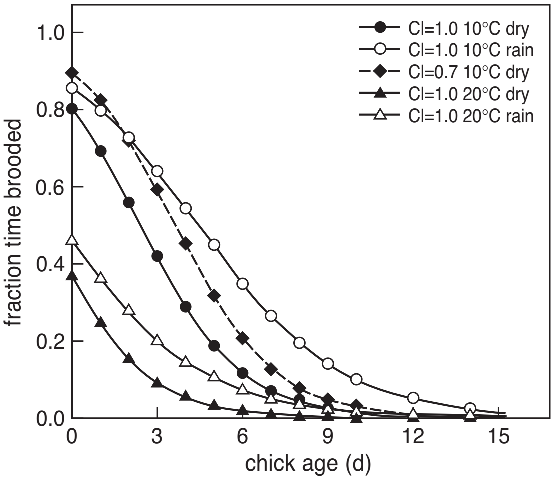


FIGURE 5.2. Brooding proportions predicted with the model in Table 5.1, illustrating effects of chick age, condition (CI), temperature and rainfall.

it may have included some unobserved resting bouts. With this proviso, we estimate that chicks older than a week usually foraged for 70-90% of the daylight period. Younger chicks are limited by brooding time, but spent at least as much of the remaining time foraging (fig. 5.1b,c). Feeding activity of older chicks seemed to be highest in the morning and lowest between 12:00 and 16:00, especially on warmer days.

The proportion of daylight time that chicks were brooded by a parent decreased with chick age and temperature but increased in the presence of rain (table 5.1, fig. 5.2). The effect of rainfall was stronger in older chicks. Wind speed did not explain additional variation in brooding proportions after temperature and rainfall had been included. Irrespective of weather conditions, chicks in poor body condition were brooded up to 20% longer than chicks in normal condition.

Foraging behaviour and age

Godwit chicks foraged by walking irregular tracks through the grassland and pecking visually located prey from the vegetation, usually in passing but sometimes after a slow 'stalking' movement. Of 18,119 ingested prey, 76% were taken from low in the vegetation, up to a walking chicks' head level, 22% from higher up, and only 1.3% from the ground, including some probing and digging into the soil. Foraging chicks did not meticulously search the vegetation but seemed to 'skim' accessible prey from stems and leaves; new items were often found during repeated passages of the same spot.

The number of prey ingested per minute foraging increased linearly during the first 7-10 days, and fluctuated around a slowly decreasing trend thereafter (fig. 5.3a, table 5.2). Proportions of prey taken from different levels remained fairly stable but 'high pecks' became more numerous in the last week before fledging (fig. 5.3b). Surface pecks and probing also increased slightly but remained rare throughout. Average size of ingested prey was estimated by combining data on time budgets, foraging success and energy expenditure of chicks (fig. 5.3c). As effects of between-day variation in energy expenditure due to weather conditions and foraging activity were not taken into account in the estimation, the general level and trajectory of values are of interest rather than day-to-day variations. These reveal a clear dichotomy, with small average prey size during the first *c.* 10 days followed by a rapid increase. The calculated average dry mass of prey of young (1-1.5 mg) and older chicks (3-4.5 mg) correspond to arthropod body lengths of *c.* 4-5 mm and *c.* 6-8 mm respectively.

Pacing rates of foraging chicks strongly increased during the first five days of life and then decreased to a stable level of c. 1.4 steps/s after two weeks. Walking speed mirrored this pattern but the decline after day 5 was counteracted by the increasing pace length of the growing chicks (fig. 5.3d). Combining the data on walking speed with time budgets yields minimum and maximum estimates of the daily distance covered during foraging. This distance increased from 3-4 km/day shortly after hatching to 9-12 km/day at 7-12 days old, and then declined to 5-10 km/day in older chicks. Over the entire 25-day fledging period, foraging chicks covered a distance of 190-260 km.

Correlates of prey ingestion rate

Effects of weather, time of day, chick condition and arthropod density on prey ingestion rate were explored with GLMMs. To account for the nonlinear increase of prey

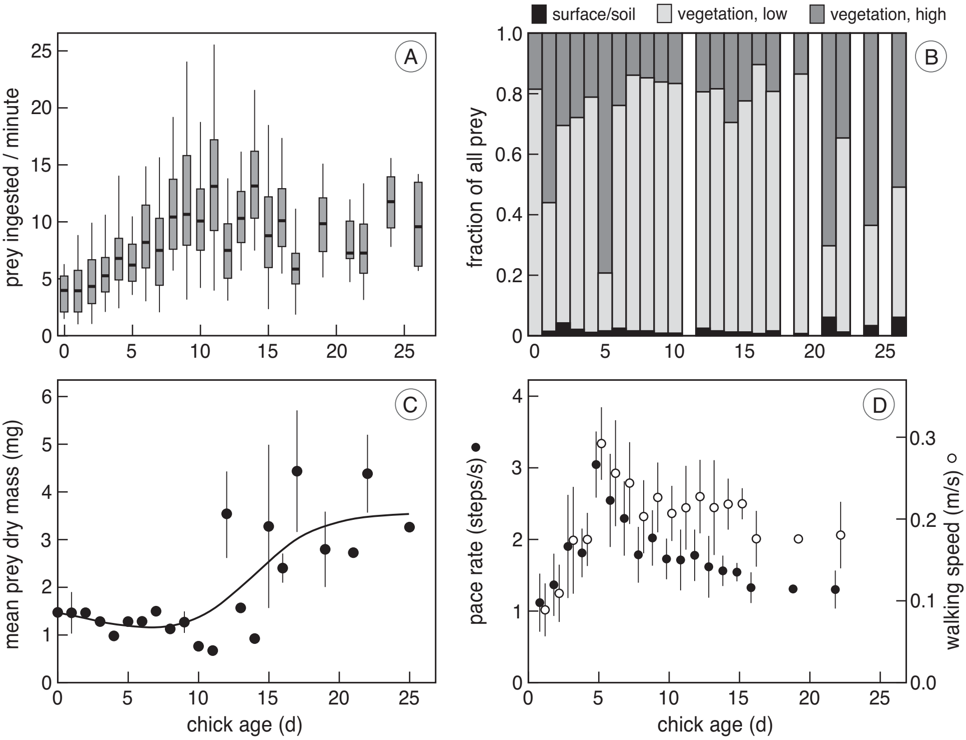
TABLE 5.2. Analysis of prey ingestion rate (prey/min) for all chicks (a) and for chicks younger (b) and equal or older than 8 days (c). Analyses started with a full GLMM including effects of age, time, time^2, T_{bs}, T_{bs}^2, windspeed, windspeed2 and rainfall (current and within last 30 min), and in (a) also all first-order interactions with age. Tables present reduced models resulting from backward elimination of insignificant terms (with regression coefficients B on the ln scale), and the effect of adding condition, total arthropod density or density of arthropods >1 mg to the reduced model. The data comprised 2269 recordings made on 41 dates in 16 chicks from 5 broods in 4 enclosures.

Fixed term	Wald statistic	d.f.	P	B	se (B)
(a) All ages combined, including interactions with age (N=2269 recordings)					
Constant				2.103	0.061
Age<8	69.95	1	<0.001	–0.0889	0.0106
Wind speed	16.62	1	<0.001	0.131	0.032
Wind speed^2	21.21	1	<0.001	–0.0155	0.0034
T_{bs}	1.45	1	0.23	–0.00850	0.00705
T_{bs}^2	0.31	1	0.58	–0.000086	0.000154
Rain	3.93	1	0.047	–0.0732	0.0369
Time	10.62	1	0.001	–0.07541	0.02314
Time^2	5.91	1	0.015	0.00202	0.00083
Age<8 x T_{bs}	3.00	1	0.083	0.00654	0.00377
Age<8 x T_{bs}^2	5.99	1	0.014	–0.000205	0.000084
Age<8 x Wind speed	18.12	1	0.105	–0.0592	0.0139
Age<8 x Wind speed^2	23.27	1	<0.001	0.0057	0.0012
Age<8 x Time	9.18	1	0.002	0.0377	0.0124
Age<8 x Time^2	9.22	1	0.002	–0.0013	0.0004
+Condition Index	2.73	1	0.10	0.3872	0.23453
+Density all arthropods	7.47	1	0.006	–0.00019	0.00007
+Density arthropods >1 mg	0.21	1	0.65	0.0006946	0.00151494
(b) Chicks <8 days old (N=946 recordings)					
Constant				1.786	0.134
Age	19.79	1	<0.001	0.0650	0.0146
T_{bs}	9.32	1	0.002	–0.00926	0.00303
Wind speed	4.24	1	0.040	–0.0227	0.0110
+Condition Index	0.29	1	0.59	0.174	0.323
+Density all arthropods	0.14	1	0.71	–0.000076	0.000204
+Density arthropods >1 mg	5.06	1	0.024	0.00997	0.00443
(c) Chicks ≥8 days old (N=1323 recordings)					
Constant				2.296	0.0760
Age	11.66	1	<0.001	–0.01910	0.00559
Wind speed	17.81	1	<0.001	0.1708	0.0405
Wind speed^2	20.84	1	<0.001	–0.02007	0.0044
Time	107.01	1	<0.001	–0.2022	0.0196
Time^2	92.23	1	<0.001	0.00671	0.00070
+Condition Index	0.03	1	0.87	–0.0458	0.27043
+Density all arthropods	1.02	1	0.31	–0.00014	0.000141
+Density arthropods >1 mg	2.29	1	0.13	0.00158	0.00104

ingestion rate, 'age' was replaced by a variable 'age<8', declining linearly from 8 on the hatching day to 0 at 8 days and all older ages. In addition to age, weather parameters and time of day significantly influenced prey ingestion rates, often nonlinearly (table 5.2, fig. 5.4). Significant interactions between these variables and 'age<8' indicated that effect sizes differed between young and older chicks; therefore separate models were constructed for chicks <8 and ≥8 days.

Prey ingestion rate was negatively correlated to wind speed and temperature, and decreased from early morning to mid-afternoon, followed by a recovery in the evening hours, particularly noticeable in older chicks (fig. 5.4a-c). However, there was strong collinearity among variables: both temperature and wind speed reached a maximum in the middle of the day (fig. 5.4d). The negative effect of wind speed on prey ingestion rate was still significant if T_{bs} and time of day were included in the model, but the effects of temperature and time of day were more strongly interchangeable. The reduced

FIGURE 5.3. Development of foraging behaviour with age. A: Prey ingested per minute of foraging (boxes give 25%, 50% and 75% quantiles, whiskers span 90% of 2269 observations). B: Fraction of prey taken from the vegetation and from the ground (N=18,119 prey). C: Average size (mg dry mass) of prey ingested. Vertical bars represent ranges based on minimum and maximum daily foraging time, dots give mid-points between these estimates, and the line is a smoothing spline (df=4) fitted through these. D: Mean (± SD) pace rate and walking speed (N=197 observations on 20 dates involving 11 chicks from 3 broods in 2 enclosures).

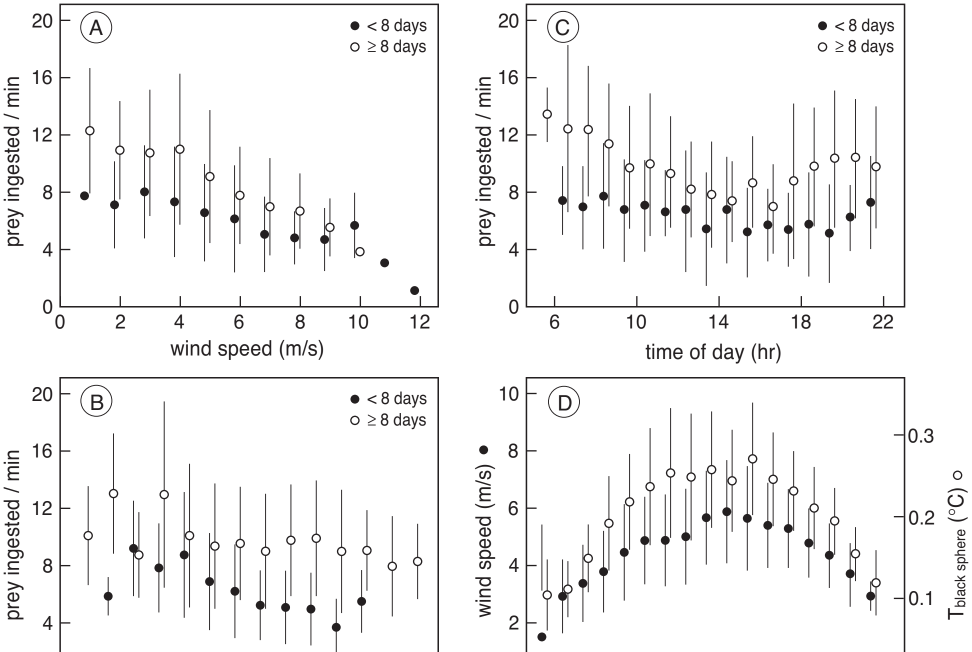


model for chicks >1 week old included, in addition to a slow decrease with age, significant nonlinear effects of wind speed and time of day; the model for younger chicks included age, wind speed and temperature (table 5.2).

By selecting only feeding observations made between 11:00 h and 17:00 h, when temperature and wind speed hardly varied with time (fig. 5.4d), the influence of (between-day) variation in these variables can be evaluated independently of any effect of time of day. In this reduced dataset (N=753 observations), prey ingestion increased with age until 8 days (W_1=51.95, P<0.001) and with wind speed (W_1=3.91, P=0.048); other variables were insignificant.

Rainfall significantly depressed prey ingestion rate (by 7%) in the combined dataset, but was not significant when age groups were analysed separately. If added to the reduced models with weather effects, feeding success was not significantly related to body condition of chicks. Total arthropod density had a small negative effect on prey ingestion rate in the combined dataset, but not in separate age groups. Prey ingestion rate of chicks up to a week old, but not that of older chicks, was positively correlated to the density of arthropods >1 mg dry mass.

FIGURE 5.4. Prey ingestion rate (grouped into classes, mean ± SD; total N=2338) of foraging godwit chicks in their first week and thereafter, in relation to wind speed (A), temperature (B) and time of day (C). D shows how wind speed and temperature varied during daylight hours.



DISCUSSION

Time budgets

Foraging and brooding were the main determinants of godwit chick time budgets. Little daylight time was spent on other behaviours, although recorded proportions may represent underestimates because chicks were out of view for part of the time. Though we cannot fully exclude the possibility, we do not think that chicks habitually forage at night. Young chicks are almost certainly brooded continuously during darkness. Older chicks, no longer brooded during daytime, regularly continued feeding until our observations ended at dusk, but the frequent contact calls between parents and young ceased when night fell (own obs.) and checks made in enclosures with a light intensifier revealed no foraging activity during darkness (G.H. Visser unpubl.). The visual foraging technique of godwit chicks may be unproductive during darkness; observed prey ingestion rates tended to drop as it grew dark (fig. 5.4c).

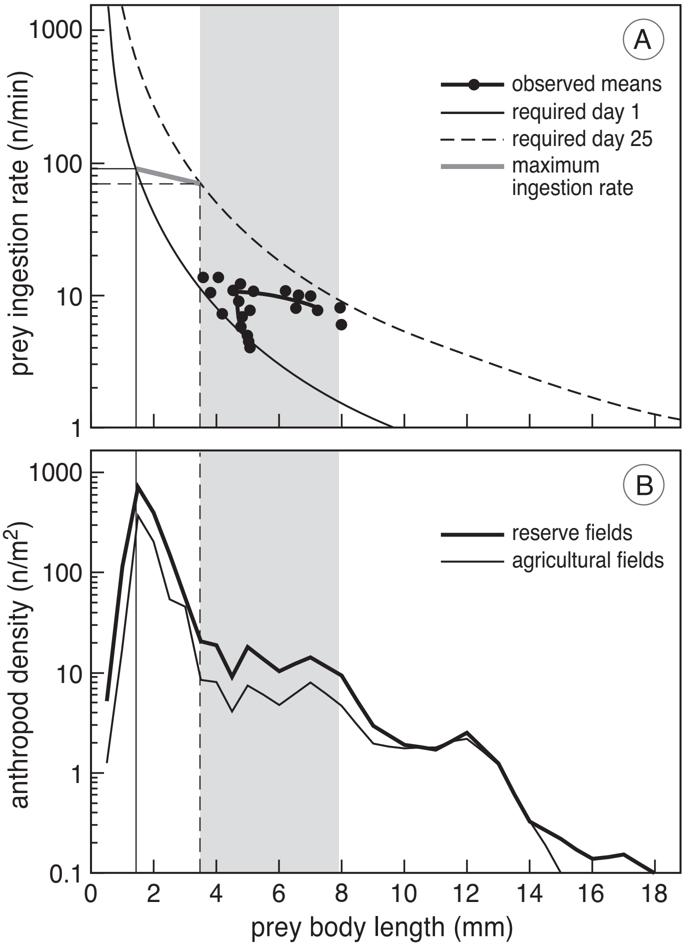
As found previously in shorebirds (Beintema & Visser 1989b, Krijgsveld *et al.* 2003, Schekkerman *et al.* 2003, Tjørve *et al.* 2007), brooding time was affected by chick age and weather. Brooding-foraging cycles in precocial chicks are mainly driven by their inability to compensate heat loss to the environment, causing a drop in body temperature (Visser 1998, Ricklefs & Williams 2003). Small size, low temperature and rainfall increase heat loss and thus shorten time between brooding bouts. Wind also increases heat loss and has been found to affect brooding proportions (Krijgsveld *et al.* 2003), but had no independent effect in our dataset, perhaps because of shelter provided by the tall grassland sward.

A novel finding was that chicks in poor body condition were brooded significantly longer than chicks showing normal mass for their age. For chicks with a condition index of 0.7, in the lower part of the range observed in the field (Chapter 8), brooding proportions increased by up to 20% depending on age and temperature. A smaller thermogenic capacity and larger surface to volume ratio may lead to a faster drop in body temperature in chicks that lag behind in growth (Visser & Hohtola 1998). The effect indicates that godwit chicks usually seek brooding out of physiological necessity rather than as a way to reduce energy expenditure when foraging needs have been fulfilled (Krijgsveld *et al.* 2003). If the latter were the case, chicks in poor body condition would be expected to prolong their foraging time by forgoing brooding opportunities, but the opposite occurred.

Chick diet

The diet of Black-tailed Godwit chicks consisted almost completely of prey taken from the grassland vegetation. Only 2% of all prey items were taken from the soil or its surface. This is in broad agreement with data from faecal analysis. Beintema *et al.* (1991) showed that godwit chicks take a wide variety of invertebrates, but typical surface and soil-dwelling taxa were found in small proportions of chicks' faeces (e.g. earthworms 13%, gastropods 17%, ground beetles 22%, rove beetles 7%, Tipulid and beetle larvae 1-2%) compared to vegetation-dwelling groups (e.g. imagines of several Diptera families 30-73%, weevils 66%, hymenopterans 78%). Although ground-dwelling species are on average larger than vegetation arthropods (Beintema *et al.* 1991), they were taken

FIGURE 5.5. Limits to prey size selection in godwit chicks. A: Observed age-specific mean prey size and ingestion rate of chicks (dots, with smoothing spline showing changes with age) set against the background of prey ingestion rates required at different mean prey sizes to sustain daily energy metabolism at hatching (day 1) and at fledging (day 25) (based on estimates of ME from Schekkerman & Visser 2001, prey energy density 23 kJ/g, assimilation efficiency 0.74, and foraging time 8 and 12.8 h/day respectively). Also shown is the trajectory over age of maximum ingestion rate of small prey predicted from chick bill length (Zwarts & Wanink 1993), with resulting minimum prey size thresholds calculated from required foraging intake rate (based on energy requirements and foraging time) at age 0 and 25 days. B: Size-density distributions of arthropods in reserve and agricultural fields during the main chick period (30 April-18 June; 110 samples in total), with predicted minimum (vertical lines) and observed mean prey sizes (grey bar) of chicks projected onto it.



in such small numbers that their contribution to the chicks' total energy and nutrient intake remained limited.

Ontogenic changes in foraging behaviour and prey size

During their first week, both foraging time and prey ingestion rate of chicks increased while average prey size remained more or less stable. After 7-10 days, prey ingestion rate levelled off. As energy demand increases until fledging and foraging time remained roughly constant after daytime brooding had ceased, prey size must have increased in the last two weeks before fledging (fig. 5.5). Such an increase was also recorded by faecal analysis in chicks of Golden Plover *Pluvialis apricaria* (Pearce-Higgins & Yalden 2004). As the average size of arthropods or the number of large individuals in our samples did not increase in the course of the spring (Schekkerman & Beintema 2007), the shift represents an increasing selectivity towards larger prey.

During the chicks' first week, walking speed increased roughly proportional to prey ingestion rate. Chicks thus increased their intake rate by searching a larger area per unit time. After 5-7 days walking speed declined to a lower level maintained until fledging while chicks took increasingly large prey. Size selection may be enhanced by walking slowly rather than by speeding up to cover more ground if this enables a more thorough search for large but cryptic prey, or if larger insects are more likely to escape when approached by a rapidly moving chick. Most larger arthropod taxa (4-20 mm) common in the diet of godwit chicks are either fast-moving animals that possibly must be stalked (e.g. dung flies Scatophagidae, house flies Muscidae, and crane flies Tipulidae), or slow-moving but cryptic (weevils Curculionidae and sawfly larvae Tenthredinidae (Beintema *et al.* 1991).

One possible explanation for the shift in mean prey size with age is that it takes time to acquire the skills required to capture larger, more 'difficult' prey (Davies 1976, Moreno 1984, Yoerg 1998, Wheelwright & Templeton 2003). Alternatively, older chicks may be forced to select increasingly large prey because the rate at which small items can be ingested becomes limiting as energy demands increase. Among shorebird species, the time needed to handle and ingest small invertebrates is related to bill length, reflecting the time needed to transport items up the length of the bill (Zwarts & Wanink 1993). We estimated the maximum ingestion rate (inverse of handling time) of small prey by godwit chicks at different ages by inserting their bill length into the equation of Zwarts & Wanink (fig. 5.5a). Optimal foraging theory predicts that animals should only ingest prey of which the profitability (energy yield per unit handling time) equals or exceeds the average energy intake rate during foraging (Stephens & Krebs 1986). We calculated the latter from energy requirements and foraging time at each age, and combined this with predicted handling time to estimate the minimum prey size that chicks should accept. This threshold size increases from 0.07 mg dry mass (corresponding to a body length of *c.* 1.5 mm) at hatching to 0.5 mg (or *c.* 3.3 mm) at fledging (fig. 5.5a). Smaller arthropods should be ignored at all times. The minimum acceptable prey sizes can be compared to the size-density distribution of arthropods in the grasslands holding the enclosures (fig. 5.5b). If chicks would ignore all prey smaller than the size threshold and take larger animals in proportion to their density, the average size of ingested prey would be *c.* 0.3 mg (2.1 mm) at age 0 and *c.* 2.6 mg (5.7 mm) at 25 days. Observed mean prey sizes were larger (resp. 1-1.5 and 3-4.5 mg, fig. 5.3c), suggesting some selectivity even above the lower acceptance threshold. It is noteworthy that the range in mean prey sizes taken by godwit chicks cover a range in the size-density distribution where available density does not decline strongly with size (and biomass per m^2 even approximately doubles). Older chicks could well be precluded from specialising on still larger arthropods (>8 mm or 4.5 mg) by the rapid drop-off in their density in the grassland vegetation (fig. 5.5b), making them impossible to find at the required rate.

Perhaps because of this limitation, godwit chicks gradually switch to a different feeding mode in the first few weeks after fledging, probing for buried invertebrates in wet grassland and water bottoms in the way adults do (unpubl.obs.). We can only speculate on why this transition does not occur earlier; perhaps the bill is still too short or vulnerable for probing in younger chicks.

Environmental correlates of foraging success

Weather conditions affected not only time available for foraging but also prey ingestion rate. Temperature and wind speed varied in parallel with time of day, but the effect of wind speed was partly independent of that of other variables, affecting prey ingestion rates negatively both within and between days. Chicks may be less able to detect or capture prey amidst moving vegetation in windy conditions, or arthropods may avoid or be blown or shaken off exposed stems and leaves where they are best visible to chicks. The less clearly independent effect of temperature on prey ingestion rate was negative both before and after correlated variation in wind speed and time of day was taken into account. Although this result may be counterintuitive given the general positive effect of temperature on larval development and emergence and activity of adult insects (Bergman *et al.* 1996, Tulp & Schekkerman 2008), it might be explained by an increase in reaction and escape speed of insects at higher temperatures. Cool conditions without wind often occur in the early morning and in the evening, explaining part of the observed diurnal pattern (fig. 5.4). Alternatively, chicks may be 'hungry' in the morning after a night without food, and could anticipate to the upcoming night by foraging more intensively in the evening. However, we found no evidence for the latter: prey ingestion rates dropped in the last hour before darkness even after controlling for wind and temperature.

This study did not find a strong effect of arthropod abundance on chick foraging success. Prey ingestion rate was not significantly correlated with total biomass of vegetation invertebrates, and even negatively with total density, though not in older chicks. Total density or biomass may be a poor predictor of prey availability because it includes many small animals that are unprofitable to chicks. Intake rate may be more sensitive to the abundance of larger prey, and a positive effect of the density of arthropods ≥1 mg was indeed observed, but only in chicks older than a week. Possibly, our weekly sampling regime – intended primarily to compare arthropod abundance between management treatments – lacked temporal resolution to reveal clearer effects. In foraging experiments conducted in the same area, Schekkerman & Beintema (2007, Chapter 6) did find a 31% lower average prey ingestion rate of chicks in cut agricultural fields, which contained 50-70% less arthropods than uncut reserve fields. Even though arthropod density varied fivefold among our observation weeks, abundance effects may have been masked by variation in availability due to factors operating on shorter time scales. In the experiment conducted by Schekkerman & Beintema (2007), this type of variation was excluded.

Vulnerability to foraging conditions

Black-tailed Godwit chicks foraged up to 70-90% of the daylight period and covered impressive distances of 3-12 km/day in the process. Schekkerman and Visser (2001) showed that this precocial lifestyle results in energy requirements exceeding those of parent-fed chicks of similar body size by 39%, mainly because of larger expenditure on activity and thermoregulation. While young godwits thus need more food than altricial chicks, their options to compensate for reductions in foraging success are limited. Activity costs can only be reduced at the expense of further reductions in food intake, while the length of the daylight period offers little leeway for foraging longer. In addition, the proportion of the total energy budget that chicks allocate to growth is relatively small (on average 26%), so that reductions in energy intake can soon result in cessation of growth or even starvation (Schekkerman & Visser 2001).

The vulnerability of godwit chicks to reductions in food availability would be further increased if a reduced body condition itself negatively affected their performance, causing them to fall further behind. We observed that chicks in poor condition were brooded more than normally growing chicks under the same conditions. The effect of this on potential foraging time may be significant in young chicks during cold and wet weather when brooding occurs most, though it is unknown if it can preclude recovery when conditions improve. We found no effect of body condition on the prey ingestion rate of chicks. It could be difficult to detect such an effect in the field, but our dataset was large and spanned the entire range in body conditions occurring in free-living chicks (Chapter 8).

Our study and work by Beintema *et al.* (1991) indicate that Black-tailed Godwit chicks growing up in agricultural grassland feed on small prey that must be available in high densities to satisfy their high energy needs within the available feeding time. The size-density distribution of arthropods in the sampled grasslands does not allow a larger average prey size than was observed, as animals >8 mm were very scarce. Might this have been different in the species' original breeding habitat, grasslands and bogs along lakes and rivers (Cramp 1983)? Larger arthropods generally are the first to disappear when intensity of agricultural grassland use increases (Kajak 1978, Siepel 1990, Blake *et al.* 1994, Britschgi *et al.* 2006), and even meadowbird reserves like our study area harbour very few large insects like grasshoppers, dragonflies and butterflies and their larvae. Possibly, the transition made by godwits to breeding in increasingly fertilised agricultural grasslands, stimulated by a high availability of soil invertebrates to foraging adults (Beintema 1986), has been associated with a loss of the most profitable prey size classes for chicks. The Black-tailed Godwit is the largest European grassland shorebird with wholly insectivorous self-feeding chicks; those of still larger species are either fed by their parents (Eurasian Oystercatcher *Haematopus ostralegus*) or start probing for soil fauna at an earlier age (Eurasian Curlew *Numenius arquata*, Beintema *et al.* 1991). It is also noteworthy that godwits have declined more strongly in Dutch grasslands than the related Common Redshank *Tringa totanus* of which the smaller chicks can more easily meet their lower daily requirements on small insects. In modern agricultural grassland, Black-tailed Godwit chicks may thus face the limits of a prey size distribution on which they can successfully fledge, and this may make them particularly vulnerable to effects on food availability of grassland management and weather.

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REFERENCES

- Beintema A.J. 1986. Man-made polders in The Netherlands: a traditional habitat for shorebirds. Colonial Waterbirds 9: 196-202.
- Beintema A.J. & G.H. Visser 1989a. The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77: 181-192.
- Beintema A.J. & G.H. Visser 1989b. Growth-parameters in chicks of Charadriiform birds. Ardea 77: 169-180.
- Beintema A.J., J.B. Thissen, D. Tensen & G.H. Visser 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. Ardea 79: 31-43.
- Bennet P.M. & Harvey P.H. 1985. Brain size, development and metabolism in birds and mammals. Journal of Zoology 207: 491-509.
- Bergman P., U. Molau & B. Holmgren 1996. Micrometeorological impacts on insect activity and plant reproductive success in an alpine environment, Swedish Lapland. Arctic and Alpine Research 28: 196-202.
- Blake S., G.N. Foster, M.D. Eyre & M.L. Luff 1994. Effects of habitat type and grassland management-practices on the body-size distribution of Carabid beetles. Pedobiologia 38: 502-512.
- Britschgi A., R. Spaar & R. Arlettaz 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: lessons for overall Alpine meadow management. Biological Conservation 130: 193-205.
- Castro G., Stoyan N. & Myers J.P. 1989. Assimilation efficiency in birds: a function of taxon or food type? Comparative & Biochemical Physiology 92A: 271-278.
- Cramp S. (ed.) 1983. The birds of the western Palearctic. 3. Oxford University Press, Oxford.
- Cummins K.W. & J.C. Wuycheck 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen Internationaler Verein Limnologie 18.
- Davies N.B. 1976. Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). Behaviour 54: 280-295.
- Heinsohn R.G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. American Naturalist 137: 864-881.
- Kajak A. 1978. The effect of fertilizers on numbers and biomass of spiders in a meadow. Symposia of the Zoological Society of London 42: 125-129.
- Krijgsveld K.L., J.W.H. Reneerkens, G.D. McNett & R.E. Ricklefs 2003. Time budgets and body temperatures of American Golden-Plover chicks in relation to ambient temperature. Condor 105: 268-278.
- Langen T.A. 1996. Skill acquisition and the timing of natal dispersal in the white-throated magpie-jay, *Calocitta formosa*. Animal Behaviour 51: 575-588.
- Moreno J. 1984. Parental care of fledged young, division of labor, and the development of foraging techniques in the northern wheatear (*Oenanthe oenanthe* L.). Auk 101: 741-752.
- Nice M.M. 1962. Development of behavior in precocial birds. Transactions of the Linnean Society, New York 8: 1-211.
- Nol E. 1986. Incubation period and foraging technique in shorebirds. American Naturalist 128: 115-119.
- Pearce-Higgins J.W. & D.W. Yalden 2004. Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European Golden Plover *Pluvialis apricaria* chicks. Ibis 146: 335-346.

- Pienkowski M.W. 1984a. Behaviour of young ringed plovers *Charadrius hiaticula* and its relationship to growth and survival to reproductive age. Ibis 126: 133-155.
- Pienkowski M.W. 1984b. Development of feeding and foraging behaviour in young Ringed Plovers *Charadrius hiaticula*, in Greenland and Britain. Dansk Ornitologiske Forenings Tidsskrift 77: 133-147.
- Ricklefs R.E. & J.B. Williams 2003. Metabolic responses of shorebird chicks to cold stress: hysteresis of cooling and warming phases. Journal of Experimental Biology 206: 2883-2893.
- Robel R.J., B.M. Press, B.L. Henning, K.W. Johnson, H.D. Blocker & K.E. Kemp 1995. Nutrient and energetic characteristics of sweepnet-collected invertebrates. Journal of Field Ornithology 66: 44-53.
- Rogers L.E., W.T. Hinds & R.L. Buschbom 1976. General weight vs length relationship for insects. Annals of the Entomological Society of America 69: 387-389.
- Rogers L.E., L.R. Buschbom & C.R. Watson 1977. Length-weight relationships for shrubsteppe invertebrates. Annals of the Entomological Society of America 70: 51-53.
- Safriel U.N., B.J. Ens & A. Kaiser 1996. Rearing to independence. In: J.D. Goss-Custard (eds.). The Oystercatcher: 219-250. Oxford University Press, Oxford.
- Schekkerman H. 1997. Graslandbeheer en groeimogelijkheden voor weidevogelkuikens. IBN-rapport 292, DLO Instituut voor Bos- en Natuuronderzoek, Wageningen.
- Schekkerman H. & G.H. Visser 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. Auk 118:944-957.
- Schekkerman H., I. Tulp, T. Piersma & G.H. Visser 2003. Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. Oecologia 134: 332-342.
- Schekkerman H. & A.J. Beintema 2007. Abundance of invertebrates and foraging success of Black-tailed Godwit (*Limosa limosa*) chicks in relation to agricultural grassland management. Ardea 95: 39-54.
- Siepel H. 1990. The influence of management on food size in the menu of insectivorous animals. Proceedings in Experimental and Applied Entomology, N.E.V. Amsterdam 1: 69-74.
- Starck J.M. 1998. Structural variants and invariants in avian embryonic and postnatal development. In: Starck J.M. & Ricklefs R.E. (eds.). Avian postnatal development: 59-88. Oxford University Press, New York.
- Starck J.M. & R.E. Ricklefs (eds.) 1998. Avian growth and development. Oxford University Press, New York.
- Stephens D.W. & Krebs J.R. 1986. Foraging theory. Princeton University Press, Princeton.
- Thorup O. 2006. Breeding waders in Europe 2000. International Wader Studies 14, International Wader Study Group, UK.
- Tjørve, K.M., H. Schekkerman, I. Tulp, L.G. Underhill, J.J. de Leeuw & G.H. Visser 2007. Growth and energetics of a small shorebird species in a cold environment: the Little Stint *Calidris minuta* on the Taimyr Peninsula, Siberia. Journal of Avian Biology 38: 552-563.
- Tulp I. & H. Schekkerman 2008. Weather- and season-related variation in the abundance of tundra arthropods: hindcasting the effect of climate change on prey availability for arctic birds. Arctic 61: 48-60.
- Visser G.H. & R.E. Ricklefs 1993a. Development of temperature regulation in shorebirds. Physiological Zoology 66: 771-792.
- Visser G.H. & R.E. Ricklefs 1995. Relationship between body composition and homeothermy in neonates of precocial and semiprecocial birds. Auk 112: 192-200.

- Visser G.H. 1998. Development of temperature regulation. In J.M. Starck & R.E. Ricklefs (eds.), Avian growth and development: 117-156. Oxford University Press, New York.
- Visser G.H. & E. Hohtola 1998. Development of locomotion and endothermy in altricial and precocial birds. In: Starck J.M. & Ricklefs R.E. (eds.). Avian postnatal development: 157-173. Oxford University Press, New York.
- Walsberg G.E. & W.W. Weathers 1986. A simple technique for estimating operative environmental temperature. Journal of Thermal Biology 11: 67-72.
- Wheelwright N.T. & J.J. Templeton 2003. Development of foraging skills and the transition to independence in juvenile Savannah Sparrows. Condor 105: 279-287.
- Yoerg S.I. 1998. Foraging behavior predicts age at independence in juvenile Eurasian dippers (*Cinclus cinclus*). Behavioral Ecology 9: 471-477.
- Zwarts L. & J. Wanink 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Netherlands Journal of Sea Research 31: 441-476.

Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management

6

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1. Effects of agricultural intensification on availability of grassland invertebrates as food for chicks of the declining Black-tailed Godwit *Limosa limosa* were studied in the Netherlands. Invertebrates were sampled with photo-eclectors in wet grasslands used for intensive dairy farming (high fertiliser input, 2-3 cuts starting early to mid-May) and in a meadowbird reserve (moderate fertiliser input, one cut in mid-June).

2. Invertebrates were slightly more abundant in reserve than in agricultural fields before the first cut of the latter. In the 4-6 weeks between the first cut of agricultural fields and that of reserve fields, invertebrates were much more abundant on reserve fields. In this period most godwit chicks are present. Mean size of arthropods was similar under the two management regimes, but large Coleoptera were more abundant in agricultural fields early in the season.

3. In a foraging experiment, captive-raised godwit chicks ingested 31% fewer prey per unit time when foraging in cut agricultural grasslands than in uncut reserve fields, a difference large enough to compromise chick growth and survival.

4. Wild broods strongly selected to stay in reserve fields, especially after agricultural fields had been cut, and travelled towards these over distances up to more than 0.5 km. Preference for reserve grasslands declined from early June onwards.

5. Postponing mowing dates, in reserves or on farmland by means of agri-environment initiatives, improves feeding and survival conditions for godwit chicks and other insectivores feeding in the grassland sward, in addition to its beneficial effect on hatching success.

INTRODUCTION

Many bird species breeding in lowland wet grasslands in Europe have suffered considerable population declines over the past few decades (Donald *et al.* 2001, Birdlife International 2004, Thorup 2006). Loss of grassland habitat and negative effects on the birds' reproductive output of increasing intensity of agricultural use, affecting fertilizer input, water tables, mowing dates, grazing densities, and habitat heterogeneity, are thought to be the main causes of these declines (Beintema 1986, Witt 1986, Beintema *et al.* 1997, Chamberlain & Fuller 2000, Vickery *et al.* 2001, Newton 2004). The precise mechanisms involved differ between species and agricultural systems (Green 1988, Baines 1990, Berg 1992, Green *et al.* 1997, Wilson *et al.* 1997, Bradbury & Bradter 2004, Newton 2004), and are not in all cases well understood. Clearly, specific knowledge is important for defining appropriate conservation measures.

The Netherlands hold internationally important populations of grassland-breeding shorebirds (Charadrii), including 47% of the European population of Black-tailed Godwit *Limosa limosa limosa* (Thorup 2006). This species has been in decline since the 1960s, and national population estimates have fallen from at least 125,000 breeding pairs around 1975 to *c.* 68,000 in 2004 (SOVON 2002, Teunissen & Soldaat 2006). The main driver of this decline, especially in agricultural grasslands where 60-75 % of the population occurs, is insufficient breeding productivity resulting from both reduced hatching success and low chick survival (Kruk *et al.* 1997, Schekkerman & Müskens 2000, Schekkerman *et al.* 2005, chapter 7).

Traditionally, research and policy concerned with conservation of Dutch grassland shorebirds focused on the survival of clutches, attempting to reduce mowing and trampling losses (Klomp 1951, Beintema & Müskens 1987, Guldemond *et al.* 1993, Kruk *et al.* 1996, Musters *et al.* 2001). The survival of chicks received attention only later (Beintema *et al.* 1991, Beintema 1995, Kruk *et al.* 1997, Schekkerman & Müskens 2000). Postponing mowing and grazing until most clutches have hatched is a major aspect of meadowbird conservation practice in The Netherlands, both in reserves and in agri-environment schemes (Beintema *et al.* 1997, Kleijn *et al.* 2001, Verhulst *et al.* 2007). A second approach has been to involve volunteers in finding and marking clutches so that losses due to farming operations and trampling can be avoided by farmers (Guldemond *et al.* 1993, Kruk *et al.* 1996). Stimulated by the government, the number of protected shorebird nests fluctuated around 127,000 in recent years, including 22,000 nests of Black-tailed Godwit (van Paassen 2006).

Though nest protection allows more clutches to hatch, general farming practice, including fertiliser use, drainage, mowing dates and stocking densities, remains unchanged, and birds may still suffer detrimental effects of agricultural intensification. Godwit chicks, like those of most other shorebirds, are precocial and nidifugous, and feed themselves on a wide range of invertebrates living in the grassland vegetation (Beintema *et al.* 1991). In addition to direct mortality due to mowing and increased predation risk after loss of cover (Chapter 8, Schekkerman *et al.* 2005), foraging conditions for chicks may be affected through changes in food availability.

A primary ingredient of intensification of agricultural grassland use is an increase of fertiliser inputs (Beintema *et al.* 1985, Vickery *et al.* 2001), which increases plant productivity and plant nutrient content, and reduces plant species diversity by a shift towards a few dominant species (Bakelaar & Odum 1978, Inouye & Tilman 1995). The total amount of nutrients available for invertebrate consumers generally increases and invertebrate abundance often responds positively to (nitrogen) fertilisation (Hurd & Wolf 1974, Haddad *et al.* 2000, Perner *et al.* 2005). However, in agricultural grasslands increased fertilizer inputs usually come with a suite of associated changes, like drainage, reseeding with grass monocultures, and intensive grazing or cutting, that may affect invertebrates in different ways (Schäfer & Haas 1979, Morris 1981a, 1981b, van Wingerden *et al.* 1992). Under intense cutting or grazing, especially larger invertebrates may have difficulties completing their life cycles. The average size of grassland arthropods may decline with increasing fertilizer input (Kajak 1978, Siepel 1990, Blake *et al.* 1994), reducing the profitability (energy gained per unit handling time) of arthropod prey for foraging chicks, and this could reduce intake rate even if total biomass was unaffected (Beintema *et al.* 1991).

While these changes occur on a time scale of years, foraging success of chicks may also be sensitive to direct, short-term effects of farming practice. Nowadays, the first spring cut of agricultural grasslands overlaps extensively with the fledging period of chicks of Black-tailed Godwit and other grassland insectivores. If cut swards contain fewer invertebrates than uncut vegetation, this will reduce food availability for chicks and may affect their growth and survival.

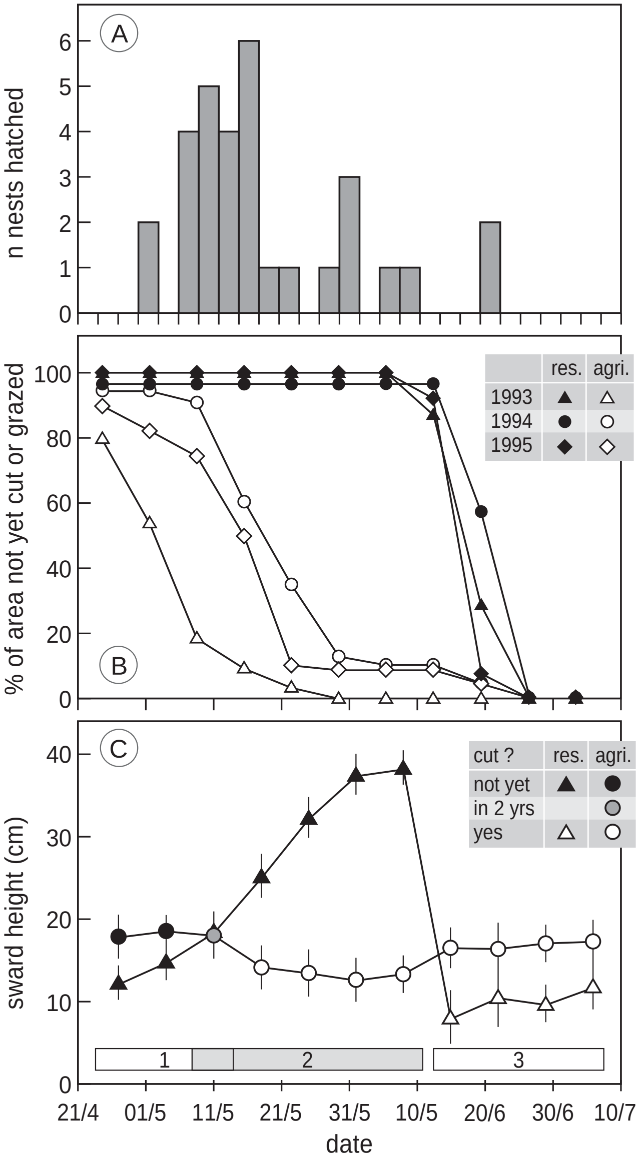
In this study, we compare food availability for and feeding success of Black-tailed Godwit chicks between grasslands managed as a meadowbird reserve and for intensive dairy farming. These situations span the range in farming intensities found in areas with substantial meadowbird populations in the Netherlands. The abundance of grassland invertebrates is examined in relation to fertilizer input and mowing regime, water table level, and season. We also experimentally compared the foraging success of godwit chicks in cut and uncut grasslands, and described habitat selection of wild godwit broods. The implications for conservation of Black-tailed Godwits and other insectivorous birds in agricultural grasslands are discussed.

MATERIALS AND METHODS

Study area and management treatments

The study was conducted in an open grassland area on clay-on-peat soils near Baarn, The Netherlands (52°12’N 15°19’E), in 1993-1996. Part of the 90 ha study site was managed as a meadowbird reserve (21 ha); the remainder was used by dairy farmers for silage production (first cut: 58 ha) and grazing (11 ha, increasing to 20-25 ha after the first cut). *Reserve management* had been in place for five years and consisted of moderate fertiliser input in the form of farmyard manure, to a total of *c.* 150 kg Nitrogen/ha/yr, including *c.* 50 kg N/ha/yr by atmospheric deposition. There was one grass cut shortly after 15 June, followed by manure application and low-intensity grazing in the summer. Ditch water levels were maintained close to field level in winter, at 0.2-0.3 m below field level in spring, and lowered somewhat further in June to facilitate mowing. Two isolated reserve fields had water tables similar to agricultural fields. Under *agricultural*

FIGURE 6.1. Seasonal patterns in 1993–1995 of (A) hatching dates of Black-tailed Godwit nests in the study area (grouped in 3-day periods), (B) percentage of the total area of reserve and agricultural fields in the study area that had not yet been cut or grazed and (C) average sward height (± SE) on sampling fields (with indication of three periods used in analyses, see text). Shading of symbols denotes whether fields had been cut.



management, fertiliser input reached 300-350 kg N/ha/yr, applied as cattle sludge and inorganic fertiliser. There were two or three silage cuts per year, the first in early or mid- to late May depending on the weather (fig. 1), and the second in June. Ditch water levels in the agricultural part were 0.4-0.8 m below field level in spring and summer and 0.6-1.0 m below field level in winter. At a few fields adjacent to the reserve area, reserve water tables were maintained.

The vegetation of agricultural fields was dominated by the grasses *Lolium perenne* and *Poa trivialis*, with a variable amount of forbs (a.o. *Taraxacum officinale, Stellaria media, Ranunculus repens, Trifolium album* and *Rumex acetosa*). On reserve fields, other grasses (a.o. *Holcus lanatus, Alopecurus pratensis* and *Anthoxanthum odoratum*), and herbs (*Ranunculus acris, Plantago lanceolata, Cardamine pratensis, Bellis perennis* and *Lychnis flos-cuculi*) were more abundant. In the study period, on average 25 ± 1 (SE) godwit breeding territories (density 120 /km^2) were present in the reserve, and 21 ± 3 (30 /km^2) in the agricultural fields.

Field characteristics and arthropod abundance

Abundance of grassland invertebrates, sward height, an abiotic field chararacteristics were measured between late April and early July in 1993-1995 – the period that godwit chicks are present in Dutch grasslands. A total of four or eight fields were sampled, one or two per combination of management (reserve or agricultural) and ditch water level (high or low). Two replications were made in periods 1 and 2 in 1994 and period 1 of 1995, one in the remaining periods (see below for definition of periods).

Sward heights were measured weekly by taking 20 readings diagonally across the plot of the height at which a polystyrene disc (Ø 50 cm) rested on the vegetation. Groundwater tables were read weekly from piezometers placed in the centre of each field. Abundance of aboveground invertebrates was sampled with photo-eclectors or 'pyramid traps' (Funke 1971), pyramidal frames with 0.25 m^2 base area, covered by black cloth with a transparent trapping jar on top containing 4% formaline solution to kill and preserve invertebrates. Five traps were placed diagonally across each field, and emptied weekly and then reset a few m away. Sampling was discontinued during some weeks to allow mowing and manure application.

In the laboratory, invertebrates were counted and identified to taxonomic levels ranging from suborder (Hymenoptera, Homoptera, Collembola) to family (other groups). Body length was measured to the nearest 0.5 mm in animals ≤ 5 mm and to 1 mm in larger ones. Lengths were converted to dry mass using (taxon-specific) equations, given in Rogers *et al*. (1976, 1977) or derived by drying and weighing own material (Schekkerman 1997). All groups except Acarina and non-sminthurid Collembola were included in the analysis.

Numbers and biomass (dry weight) of invertebrates were expressed per m^2 and log-transformed before analysis to normalise the data. Mean dry mass of individual invertebrates was calculated by dividing the total dry weight by the number of individuals in each sample. Data were analysed with Linear Mixed Models (LMM; REML directive in Genstat v.8), with field, year and week as random variables to take into account that the same fields were sampled repeatedly over time. Differences between management categories were tested by including management type and water level (and their interaction) as fixed variables. Based on mowing schedules under the two management treatments, the season was divided into three periods. The first period comprised two weeks before any of the fields had been cut. The second period covered 2-4 weeks in which all agricultural fields had been cut once (on 8-23 May) but reserve fields not yet. The third period ran from the first cut of the reserve fields (on 15-20 June, coinciding with the second cut of agricultural fields in two of the three years) until early July (2-3 weeks). The length of the periods differed between years, but periods included the same sampling weeks for all fields within a year.

Foraging experiment

In the main period of chicks' presence (period 2 of the invertebrate survey), foraging success of chicks was compared experimentally between (uncut) reserve and (cut) agricultural fields. In May 1995, five godwit eggs were collected from three clutches in the study area and hatched in an incubator. At age 1-2 days, the chicks were placed in grassland in an outdoor aviary of 5 x 10 m, with a small indoors section heated by an infrared lamp. Water and food (chicken pellets, supplemented with a small amount of live insects) were available *ad libitum*. Nevertheless, chicks spent most of the day searching for invertebrates in the grass of the aviary. Foraging experiments started when the chicks had become homeothermic at outdoor temperatures. After fledging, chicks were released into the field.

There were nine experimental days between 23 May and 5 June, with chicks aged 10-23 days (fledging occurs at 24-26 days). Each day consisted of two sessions. Each of two pairs of chicks was placed in a 50 m^2 circular wire-netting enclosure, either in a reserve field or in an agricultural field (both N=9). In the next two hours, an observer seated beside the enclosure at a height of 2 m made 20 one-minute recordings of foraging rate and 10 recordings of walking speed on each chick. After a break of 1-1.5 h, the chick pairs were exchanged between fields and a second foraging session was held. Pairs were used because chicks often stopped feeding after a while if released into the enclosures alone. The composition of pairs was rotated between experimental days. All observations were made between 10:00 h and 17:00 h, as feeding rate is relatively constant over this period of the day (Chapter 5).

Foraging rate was defined as the number of prey items ingested per minute. Most prey were too small to be identified to type or size, but the swallowing movements were usually clearly visible. For each prey the height at which it was captured was recorded as 'high' (from vegetation higher than a walking chicks' head level), 'low' (from vegetation at or below head level), or 'ground' (taken from the ground). Between sessions, observers moved together with the chicks, so that observer differences are aliased with differences between chick pairs and not with management type. Observer effects were explicitly accounted for in the statistical analysis.

Foraging rate and walking speed (steps/min) were analysed with a Linear Mixed Model (LMM) containing field type (reserve or agricultural) and session (morning and afternoon) as fixed variables and chick identity, observer and experimental day (with interactions) as random variables. Data were log-transformed before analysis.

To obtain an indication of the abundance and size distribution of grassland arthropods at the time and site of the experiments, four yellow 'sticky boards' (10x25 cm, adhesive on both sides) were placed vertically in the vegetation just outside the experimental enclosures at the start of the first session of each experimental day. After the second session, boards were collected and trapped arthropods were counted and their body length estimated. Sward height was measured in all experimental enclosures. Arthropod numbers (log-transformed) and sward height were compared between management types using analysis of variance, with experimental day as a blocking factor.

Habitat use of broods

During weekly censuses of the study area between mid-April and late June 1993-1996, all Black-tailed Godwit pairs seen with chicks or giving alarm calls that reveal the presence of chicks were plotted on maps. The distribution of five grassland types was recorded simultaneously. Fields were classified as ‘reserve’ or ‘agricultural’ type, with either low (≤ 15 cm) or high (> 15 cm) vegetation, or as ‘grazed’ by livestock (starting on the date that animals were introduced). Vegetation height on grazed fields depended on the time that animals had been present. Densities of godwit broods in different grassland types were analysed with Generalised Linear Models (GLM) with Poisson distribution and a log link function. To describe temporal changes in habitat use, the spring was divided into three periods, analogous to the invertebrate survey (fig. 6.1).

RESULTS

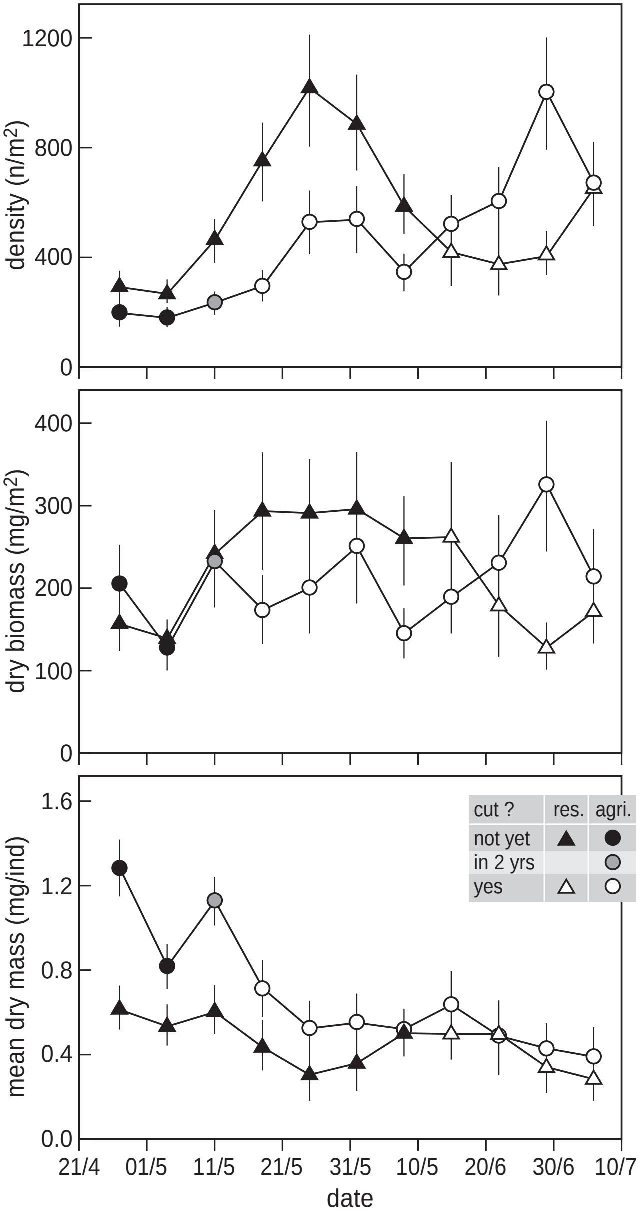
Sward height and water table

Groundwater depth reflected the orthogonal setup and differed between fields with high and low ditch water levels (means 43 ± 4 cm (SE) vs. 57 ± 2 cm below field level, N=8 fields, ANOVA: $F_{1,6}$=6.75, P=0.06), but not between reserve and agricultural fields ($F_{1,6}$=0.06, P=0.83, interaction water level x management $F_{1,6}$=0.17, P=0.70). Early in the season sward height was slightly larger on agricultural fields than on reserve fields (fig. 6.1), especially on the dry ones (period 1, LMM, Wald test, effect of management type χ^2_1=20.7, P<0.001, water level χ^2_1=20.6, P<0.001, interaction χ^2_1=0.27, P=0.60). After cutting of the agricultural fields, the sward was much taller on (especially the dry) reserve fields (χ^2_1=118.6, P<0.001), while the effect of water level was no longer significant (χ^2_1=3.31, P=0.07). Sward height within agricultural fields showed a repeated saw-tooth pattern with maxima of 18-25 cm before cutting, but this does not show in figure 6.1 as fields were cut on different dates. With the first cut in the reserve and the second cut on agricultural fields, differences in sward height disappeared (χ^2_1=1.67, P=0.20).

Invertebrate abundance

Diptera (55%), Hemiptera (13%), and Araneae (12%) were the most numerous taxa in the invertebrate samples (total N=93,793 animals), while Coleoptera (5%, mainly Staphylinidae) were important in terms of biomass (31%). At the taxonomic levels considered, there was little difference in arthropod diversity between management types. Of 73 families/suborders identified, nine were exclusive to reserve fields, four of these occurring there regularly though in low numbers (Ephemeroptera, Trichoptera, Neuroptera

FIGURE 6.2. Average (± SE) total density, biomass, and mean individual size of arthropods caught in pyramid traps in reserve and agricultural fields, per week in 1993-1995. Shading of symbols denotes whether fields had been cut.



and Lepidoptera-Nitidulidae). Four were found only in agricultural fields, with at most two specimens. There were a further nine groups of which the overall mean biomass was at least five times higher in reserve fields than in agricultural fields; there were no groups in which the reverse occurred.

The total abundance of grassland invertebrates showed strong seasonal variation that differed between reserve and agricultural fields, and in which cutting dates marked transitions in the management type with the highest abundance (fig. 6.2; LMM, effect of period on density $\chi^2_2=47.8$, $P<0.001$, on biomass $\chi^2_2=3.79$, $P=0.023$, period x management interaction both $\chi^2_2>12.9$, $P<0.001$). Therefore, effects of management type and water level were tested separately for each period. Before any fields were cut (period 1), total density of vegetation-dwelling arthropods was higher in reserve fields than agricultural fields (table 6.1). This was reflected in the means for most major invertebrate groups, except for Coleoptera. Beetles tended to be more numerous in agricultural fields, and due to their large size reversed the difference in total invertebrate biomass. After the first cut of agricultural fields (period 2), total densities and biomass were 2-3 times as large on reserve fields as on agricultural fields. Though the difference in biomass was only close to significance, it was apparent in all major taxa. After reserve fields had been cut as well (period 3), there was a tendency towards higher abundance on the agricultural fields, but differences were not significant, possibly due to the small sample size. Very similar results were obtained when only animals ≥1 mg dry mass, most profitable and most selected as food by godwit chicks (Beintema *et al*. 1991, Schekkerman 1997), were included in the analysis (results not shown).

TABLE 6.1. Abundance of invertebrates in reserve and agricultural fields in three periods in spring. Means (± SE) of total density (n/m²) and biomass (mg dry weight/m²) are given, as well as mean biomass of the most important taxonomic groups. If differences between management types exceed 30%, the higher number is printed bold.

	Period 1 (all fields uncut)			Period 2 (agricultural fields cut, reserve uncut)			Period 3 (all fields cut)		
	N=8 fields, 34 samples			N=8 fields, 40 samples			N=4 fields, 28 samples		
	reserve	farm	P	reserve	farm	P	reserve	farm	P
total density	**288 ± 34**	191 ± 23	0.01	**731 ± 207**	297 ± 84	0.02	585 ± 203	880 ± 305	0.36
total biomass	147 ± 28	182 ± 36	0.43	**307 ± 108**	118 ± 42	0.06	218 ± 78	**319 ± 114**	0.44
biomass Araneae	**16 ± 6**	9 ± 4	0.30	**12 ± 8**	1.7 ± 1.0	0.02	64 ± 39	51 ± 30	0.77
biomass Diptera	**59 ± 9**	41 ± 6	0.07	**110 ± 44**	29 ± 12	0.01	71 ± 35	**113 ± 56**	0.49
biomass Coleoptera	41 ± 14	**99 ± 35**	0.07	**126 ± 46**	67 ± 25	0.22	8.2 ± 7.0	**20 ± 16**	0.40
biomass Hymenoptera	**4.0 ± 0.9**	1.1 ± 0.3	<0.001	**13 ± 3**	8.3 ± 2.1	0.22	7.7 ± 4.6	7.6 ± 4.5	0.99
biomass Aphidoidea[1]	3.0 ± 1.4	2.7 ± 1.3	0.85	**20 ± 8**	2.7 ± 1.1	<0.001	4.2 ± 4.6	**15 ± 16**	0.35

[1] including Collembola of the family Sminthuridae

The above points to the importance of sward height in determining abundance of vegetation-dwelling grassland arthropods. Arthropod biomass increased with sward height, and neither cutting status nor management type had a significant additional effect once this was accounted for (fig. 6.3). Nevertheless, sward height alone was a rather poor predictor of arthropod biomass, explaining 21% of the total variation in the data.

Differences in invertebrate abundance between 'wet' and 'dry' fields were not significant (all P≥0.09), with one exception: Diptera biomass was twice as high on dry as on wet fields in period 1 (χ^2_1=9.21, P=0.002). Interaction effects between management type and water level were not significant.

Size distribution of invertebrates

The mean individual (dry) mass of grassland invertebrates was larger on agricultural fields than on reserve fields in the early part of the season (fig. 6.2), but this difference disappeared in May as the mean size of animals decreased (LMM, period χ^2_2=25.5, P<0.001, management χ^2_1=8.73, P=0.003, management x period χ^2_2=8.06, P<0.001). Already in period 2 the effect of management type was no longer significant. It was caused mainly by differences between management types in relative abundance of taxa containing large (Coleoptera) and small animals (Hymenoptera, aphids), but the decline in average size over time was also caused by changes in size composition within major taxonomic groups (mean size of Diptera and spiders largest in period 1, of beetles largest in period 2 and smallest in period 3, all P<0.005). During the main period of godwit chicks' presence in Dutch grasslands (early May to mid-June), the overall mean individual dry mass of arthropods was 0.44 ± 0.07 mg on reserve fields and 0.53 ± 0.07 mg on agricultural fields. Water table level had no significant effect on the mean size of grassland invertebrates (χ^2_1=1.65, P=0.20).

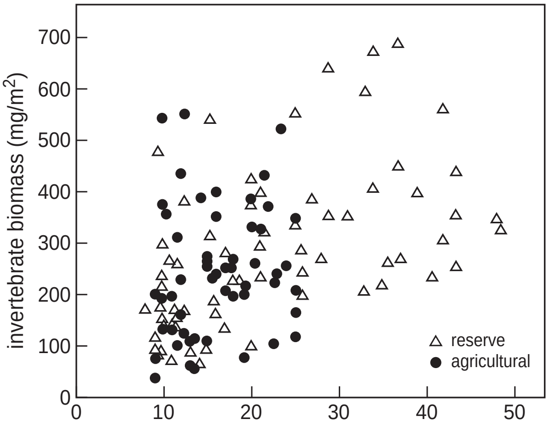


FIGURE 6.3. Relationship between arthropod biomass and sward height on reserve and agricultural fields sampled repeatedly over time. Arthropod biomass increased with sward height (fixed variable in LMM with field and year as random factors, χ^2_1=29,9, P<0.001; ln(y) = 4.90 +0.027x, R^2=0.21), and neither cutting status (cut or uncut, χ^2_1=1.42, P=0.23) nor management type (reserve or agricultural, χ^2_1=0.02, P=0.89) had a significant additional effect once sward height was accounted for.

Foraging success of chicks

The agricultural fields included in the foraging experiment had already been cut and the vegetation was in varying stages of regrowth. Average sward height was 53% higher on the still uncut reserve fields than on agricultural fields. The average total number of insects caught on sticky boards during the experiments did not differ between reserve and agricultural fields, but animals > 4 mm body length, most important in the chicks' diet, were twice as abundant in reserve fields (table 6.2).

The foraging behaviour of experimental chicks closely resembled that of chicks in natural families, observed in reserve grasslands in enclosures measuring 0.2-0.6 ha (Chapter 5). Of 9,725 prey eaten by 'wild' chicks older than 9 days, 20.6% were taken high in the vegetation, 78.1% low in the vegetation and 1.3% from the ground. For experimental chicks in reserve fields, these proportions were similar (15.2%, 81.5% and 3.3%, N=4,565). Foraging rate of experimental birds was on average slightly lower than shown by wild chicks at the same age and time of day (GLM, $F_{1,25}$=6.00, P=0.022), but within the same range of variation (range of daily means for experimental chicks: 4.7-8.0 prey/min, N=9, for wild chicks 3.7-12.1, N=16). Belting & Belting (1999) observed similar foraging rates of 5-9 prey/min in wild godwit chicks.

On eight out of nine experimental days, the chicks' foraging rate was lower in the agricultural field than in the reserve field. Over the entire experiment, mean foraging rate was 31% lower in agricultural fields (table 6.2). The difference was most pronounced for arthropods captured high in the vegetation (81% lower in agricultural fields), probably as a direct result of the shorter sward, but capture rate of prey from the lower vegetation level was reduced as well (by 26%). There was no significant difference in the rate at which prey were taken from (near) the ground. The reduction in feeding rate occurred despite a 17% higher walking speed in agricultural fields (table 6.2). Hence, 41% fewer prey were ingested per distance searched in agricultural than in reserve fields.

TABLE 6.2. Results of the foraging experiment. Means (± SE) over nine experimental days for foraging rate and walking speed of chicks, and sward height and insect numbers caught on sticky boards in the experimental enclosures.

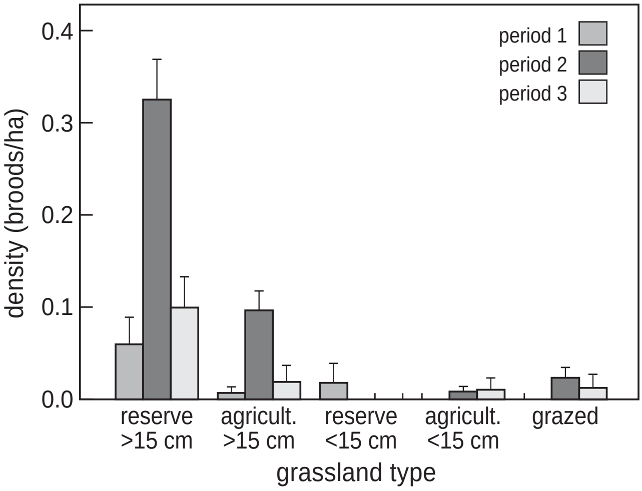
	Reserve (uncut)	Agricultural (cut)	test	P
foraging rate (prey/min)	6.06 ± 0.72	4.19 ± 0.50	χ^2_1=156.9	<0.001
from high vegetation (prey/min)	0.44 ± 0.14	0.09 ± 0.03	χ^2_1=255.9	<0.001
from low vegetation (prey/min)	4.08 ± 1.18	3.02 ± 0.88	χ^2_1=55.0	<0.001
from ground level (prey/min)	0.07 ± 0.01	0.07 ± 0.01	χ^2_1=0.27	0.60
walking speed (steps/min)	68.4 ± 4.0	79.9 ± 4.6	χ^2_1=44.5	<0.001
sward height (cm)	29.7 ± 1.7	19.4 ± 1.4	$F_{1,8}$=19.8	0.002
total arthropods (n/board)	204 ± 33	213 ± 35	$F_{1,8}$=0.03	0.86
arthropods >4 mm (n/board)	53 ± 10	27 ± 5	$F_{1,8}$=6.67	0.032

Habitat use of broods

The average total number of godwit broods in the study area was much higher in period 2 (8.8 ± 1.5 broods), than in periods 1 (1.1 ± 0.7) and 3 (2.2 ± 1.3) (fig. 6.4). GLMs revealed significant effects on brood density of both period ($F_{2,105}$=28.3, P<0.001) and grassland type ($F_{4,105}$=30.4, P<0.001). Densities were significantly higher in reserve grasslands with sward height >15 cm than in all other types (pairwise differences, *t* ≥2.50, P≤0.014), and significantly higher in agricultural fields >15 cm than in grazed fields (*t*=2.07, P=0.041) and agricultural fields <15 cm (*t*=3.03, P=0.003). Hence, godwit broods selected the highest vegetations available, which until cut in mid-June were located on reserve fields. In period 3, uncut reserve fields were no longer available and the remaining broods were found in agricultural fields with a regrowing sward (≥15 cm) and grazed fields (fig. 6.4).

In the period of maximum brood abundance (period 2), broods were more concentrated in the reserve part of the study area (67%, N=137, years combined) than were the breeding territories (54%, N=185; G^2_1=6.13, P=0.02). The maximum number of 23 broods observed in the reserve area on a single day exceeded the number that had hatched here in that year (14-17). Hence, broods actively moved towards the reserve when agricultural fields were mown. Such movements were repeatedly observed in the field, the birds sometimes arriving from distances in excess of 500 m. However, the preference for reserve fields over agricultural grasslands declined somewhat in the last 10 days before cutting of the reserve fields in mid-June, and some late broods that hatched on reserve fields were seen to move to agricultural grasslands with a sward that had regrown to >15 cm.

FIGURE 6.4. Mean density (± SE) of godwit broods in three periods during spring in five types of grassland: reserve and agricultural meadows with sward height lower and higher than 15 cm, and grazed pastures (sward height usually <15 cm). Nine, 13 and 4 censuses were made in the three periods respectively in 1993-1996, involving 10, 132 and 9 broods.



DISCUSSION

Arthropod abundance and size

The photo-eclectors provide useful estimates of food availability for godwit chicks, as they sample the density of a wide range of vegetation-dwelling arthropods, and their efficiency is less dependent on vegetation structure than that of suction samplers or sweep nets. Photo-eclectors did not capture many invertebrates that live on the grassland floor (e.g. Lycosid spiders, Carabid beetles, and slugs), but in this they resemble godwit chicks, that take more than 95% of their prey from the vegetation layer. The mean dry mass of prey taken by chicks increases from *c.* 1 mg at hatching to 3.5 mg at fledging, roughly corresponding to body lengths of 4-7 mm (Chapter 5), but faecal analysis has shown that almost all major invertebrate taxa found in grasslands, from 1.5 mm aphids to beetles and craneflies ≥15 mm, occur in the diet (Beintema *et al.* 1991), so that the use of a broad-range sampling technique is justified. Nevertheless, chicks may actively select or avoid certain types of invertebrates while foraging.

In addition to grassland arthropods, godwit chicks sometimes feed on earthworms and soil-dwelling larvae of craneflies (Tipulidae) and other insects. However, remains of soil fauna are found in only a small fraction (2-13%) of godwit chick faeces (Beintema *et al.* 1991), and probing into the soil does not become an important feeding technique until after fledging (Chapter 5). Chicks did occasionally take slugs (Limacidae and Arionidae, Gastropoda), and these reached ≥10 times higher densities in the reserve than in agricultural fields (based on pitfall trapping, Schekkerman 1997).

This study revealed large seasonal variation in the abundance of grassland invertebrates and differences between management types that were associated with the mowing regime of the fields. The effect of management was largest in period 2, when total densities and biomass were 2-3 times as large on the uncut reserve fields as on the agricultural fields that had been cut in early to mid May. Short-term effects of cutting thus were a major factor affecting invertebrate abundance. Similar results were obtained by Struwe-Juhl (1995) by sweepnet sampling. Removal of a large part of the vegetation results in the disappearance of much of the entomofauna, and some time is needed for populations to recover (Andrzejewska & Gyllenberg 1980). For Black-tailed Godwits, this short-term effect is highly relevant, as mowing dates in agricultural grasslands coincide with hatching of the chicks (fig. 6.1).

Long-term effects of management on arthropod abundance are not always so straightforward (Schäfer & Haas 1979) and may depend on the species (e.g. Morris 1981a,b). In the current study, they should be most apparent before either type of fields had been cut. In period 1, the total density of arthropods was higher on reserve fields, but this was not reflected in biomass because large Coleoptera (especially rove beetles Staphylinidae) were more numerous on agricultural fields. Their low presence in faeces (7%, Beintema *et al.* 1991) suggests that rove beetles are not frequently eaten by godwit chicks. Diptera, which dominate the chicks' diet numerically, did reach a significantly higher biomass on reserve fields. There was a non-significant trend in the same direction in three of the four other major arthropod taxa. Hence we found indications for both a short-term and a long-tem negative effect of high-intensity agricultural grassland use on the abundance of invertebrates as food for chicks (*cf.* Atkinson *et al.* 2006).

Although arthropods tended to be more abundant on dry than on wet fields, the differences did not reach significance at the replication level of this study. However, low water tables generally lead to early mowing as a result of earlier vegetation development and enhanced access for heavy machinery (e.g. Guldemond *et al.* 1995). Because of the large reduction of invertebrate abundance due to early mowing, the net impact of lowering water tables on food supply for chicks will usually be negative.

Siepel (1990) reported a strong decline in the mean weight of grassland arthropods over fertiliser levels of 0, 50 and 400 kg N/ha/yr, mainly due to the disappearance of larger species. Similar effects were found by Kajak (1978) in spiders and by Blake *et al.* (1994) in ground beetles. In contrast, this study found a larger mean size of arthropods on heavily fertilised agricultural fields than on reserve fields in the early part of the chick period, but the difference between management types was small and was caused mainly by large beetles that are not a frequent prey of chicks. The same photo-eclectors were employed in both studies, but (Siepel 1990) sampled grasslands on sandy soils and over a longer season (April-September). Comparing the results despite these differences suggests that the relationship between invertebrate size distribution and fertiliser input may be nonlinear, with the largest change occurring at fertiliser levels below 100 kg N/ha/yr (fig. 6.5). Further work is needed to confirm this pattern, but it would mean that scope for influencing prey size through management is limited in Dutch agricultural grasslands, as such low fertiliser inputs are nowadays found mainly in nature reserves.

Chick foraging success

Total invertebrate abundance may be a poor indicator of feeding conditions for chicks, if intake rates are constrained by other foraging factors such as handling time or the fraction of the total fauna that is available to chicks, or by conflicting interests such as vigilance for predators. The foraging experiment however confirmed that the lower abundance of grassland invertebrates in (cut) agricultural fields than in reserve fields in period 2 translated into a lower foraging rate of chicks. Prey ingestion rate of the experimental chicks was on average 31% lower in the agricultural fields. The difference was even larger (41%) when expressed relative to the area searched, due to the higher

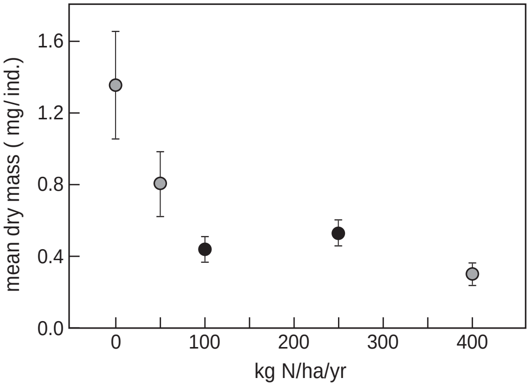


FIGURE 6.5. Relationship between fertiliser Nitrogen input and individual dry mass (mean ± SE) of grassland arthropods as sampled with photo-eclectors by Siepel (1990, grey dots) and in this study

walking speed in agricultural fields. It is not clear whether this higher speed was an attempt to compensate for a lower prey density, or a result of mechanical constraints on walking in the taller vegetation of the reserve fields. Although the size of the enclosures affected the experimental chicks' foraging behaviour to some extent (they spent part of the time walking along the fence), their prey ingestion rate in uncut fields was within the range of that of wild chicks, suggesting that the foraging rate of the hand-raised chicks was a useful indicator of foraging conditions at least in a comparative sense.

We measured feeding rate of chicks as the number of prey ingested per unit time, but most items taken were too small to estimate their size. Theoretically, the experimental chicks could have compensated for the lower ingestion rate by taking larger prey in agricultural fields. Because no significant difference in the mean size of invertebrates was found between management types in the photo-eclectors in period 2, and the sticky board samples indicated that larger insects (> 4 mm) were more abundant in the reserve fields at the time of the experiments, any such differences in prey size would have to result from active selection by the chicks. This could improve foraging success only if chicks foraged suboptimally in reserve fields, depressing their intake rate by taking too many small prey. It seems therefore unlikely that compensation occurred and the prey ingestion rate of foraging chicks probably reflected energy intake.

Field selection by broods

The better feeding conditions in (uncut) reserve grasslands were reflected in the habitat selection of godwit broods. The majority of broods were found in reserve fields, both before but especially after agricultural grasslands were cut, and active movements toward reserve fields occurred over distances of several 100s of meters. Grasslands with a sward height below 15 cm, including most grazed fields, were avoided as long as taller grass was available. In addition to offering the best feeding opportunities, tall vegetation provides shelter from wind (Klaassen 1994), and protective cover from predators (Whittingham & Evans 2004, Schekkerman *et al.* 2005, Chapter 8). The small chicks are less visible in tall grass, while predator detection is probably less affected as this is mainly done by the larger parents. These benefits are all correlated with sward height, so that their relative importance cannot be easily judged.

The preference for uncut reserve grasslands became less strong from early June onwards. At this time the vegetation of the reserve fields had grown quite tall (fig. 6.1), and started to flatten due to wind and rainfall. In addition, invertebrate abundance in the uncut reserve fields started to decline from the end of May onwards (fig.6.2), especially in the year with the earliest vegetation development. As herbs stop flowering and seed-set and lignification occur in the grasses, phytophagous invertebrates decline in reaction to the reduction of their food resources (Andrzejewska & Gyllenberg 1980). Foraging in uncut grasslands thus becomes less profitable for chicks later in the season, due to physical obstruction by the vegetation and a reduction in prey availability.

Implications for chick growth and survival

Due to the mobility and strong habitat preference of godwit families, the effect of management on growth and survival of chicks could not be measured directly by comparing broods raised in different grassland types. No broods in the study area stayed in cut agricultural fields throughout the fledging period; all moved to uncut (reserve) fields permanently or intermittently. However, some insight into the potential consequences of intensive farming for godwit chicks can be gained from energetic considerations.

Schekkerman & Visser (2001, Chapter 2) constructed energy budgets for godwit chicks on the basis of laboratory and field measurements and found that only 27% of the total energy metabolised up to fledging is allocated to growth (decreasing from 50% shortly after hatching to 15% at fledging). The remaining part of the budget, consisting of maintenance and activity, cannot be substantially economised upon in periods of food shortage, because food intake is inevitably tied to activity in the self-feeding chicks. Scope for compensating a reduced intake rate by foraging longer is also limited, as godwit chicks already spend *c.* 80% of the daylight period foraging even in reserve grasslands (Chapter 5). This implies that reductions in foraging success may quickly result in insufficient energy being available for growth.

The 31% difference in feeding rate between reserve fields and agricultural fields observed in our experiment is of similar magnitude as the growth component in the chicks' energy budget. Effects on growth and survival are therefore to be expected, especially during inclement weather, when foraging success is already reduced (Schekkerman 1997) and feeding time for young chicks is constrained by an increased need for brooding (Beintema & Visser 1989). Godwit chicks carry only small fat reserves and starve within a few days without food (Chapter 2). In addition, a poor body condition may increase the risk of predation (Swennen 1989), or parasitic infection and disease (Gershwin *et al.* 1985, Lochmiller *et al.* 1993), while a reduced growth rate delays fledging and prolongs the period of vulnerability to predators and mowing machines.

Management implications

This study has shown that modern intensive dairy farming, as found over much of the grassland area of the Netherlands, negatively affects feeding conditions for Black-tailed Godwit chicks. Fewer invertebrates occur in the vegetation of intensively used agricultural grasslands in comparison to reserve grasslands, especially after cutting. Current cutting dates in agricultural grassland approximately coincide with the peak of hatching of young godwits (fig. 6.1). In addition, the timing of the first cut and the hatching dates of godwit chicks are correlated between years, as both vegetation development and godwit laying dates are sensitive to spring temperature (Kruk *et al.* 1996). A large proportion of chicks in agricultural areas are thus born into a situation in which many fields have already been cut and offer a reduced food supply. Foraging success is sufficiently reduced in these grasslands to compromise the chicks' growth and survival.

The preference for tall vegetation puts godwit chicks at risk of being killed directly during mowing, though a significant proportion are able to escape the machines (Kruk *et al.* 1997). Surviving broods respond to the loss of shelter and feeding habitat by moving to uncut fields, but increased mechanisation and the shift from hay to silage production have led to increasingly large areas of grassland being cut within a short period. Any uncut refuges may become too small to accommodate all broods, and chicks in isolated pockets of tall vegetation may suffer increased predation risk. Recent studies confirmed that the survival of Black-tailed Godwit chicks is positively correlated with the proportion of late-cut grasslands in the breeding area (Schekkerman & Müskens 2000, Chapter 7).

These results indicate that conservation measures that increase hatching success, such as nest protection, will be ineffective for Black-tailed Godwits unless they are accompanied by measures promoting chick survival. Agri-environment schemes in which farmers postpone the first cut of grasslands should improve survival of godwit chicks outside reserves, in addition to their merit in reducing egg losses. By mid-June (or a week later in the North of the country; Beintema 1995) the majority of chicks have fledged, and the uncut swards have become less attractive to the remaining broods, so that further postponement of cutting does not yield benefits for godwits, although it may do so for other bird species. The magnitude of the short-term effects of cutting on invertebrate abundance found in this study shows that late mowing improves feeding conditions for insectivorous birds even when no changes in fertiliser use or water table occur, although the sampling results in period 1 suggest that benefits increase on a longer term when fertiliser input is reduced and a more diverse vegetation develops.

Other insectivorous grassland birds such as Eurasian Curlew *Numenius arquata*, Common Redshank *Tringa totanus,* Ruff *Philomachus pugnax* and certain passerines may be affected in the same way as Black-tailed Godwit chicks, although others like Northern Lapwing *Vanellus vanellus* and Common Starling *Sturnus vulgaris* forage more profitably in short swards (Devereux *et al.* 2004). Adult godwits, which feed by probing for soil invertebrates, similarly show a preference to feed in shorter swards, and occasionally leave their brood in their mate's care to feed in nearby cut fields (unpubl. data). The proximity of differently managed fields within the same area may thus allow different bird species and age classes to each use their preferred grassland type (Benton *et al.* 2003). Godwit broods actively migrate towards the late-mown 'refuges' within heterogeneous landscapes, and this will also enhance the effectiveness of nest protection carried out in the surrounding fields. The desired spatial configuration of such 'management mosaics' depends on the maximum density at which broods can co-occur and the distances that they can safely bridge, and deserves further study.

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REFERENCES

- Andrzejewska L. & G. Gyllenberg 1980. Small herbivore subsystem. In A.I. Breymeyer & G.M. van Dyne (eds.), Grasslands, systems analysis and man: 201-267. Cambridge University Press, Cambridge.
- Atkinson P.W., R.J. Fuller, J.A. Vickery, G.J. Conway, J.R. Tallowin, R.E.N. Smith, K.A. Haysom, T.C. Ings, E.J. Asteraki & V.K. Brown 2006. Influence of agricultural management, sward structure and food recources on grassland field use by birds in lowland England. Journal of Applied Ecology 42: 932-942.
- Baines D. 1990. The roles of predation, food and agricultural practice in determining the breeding success of the Lapwing (*Vanellus vanellus*) on upland grasslands. Journal of Animal Ecology 59: 915-929.
- Bakelaar R.G. & E.P. Odum 1978. Community and population level responses to fertilization in an old-field ecosystem. Ecology 59: 660-665.
- Beintema A.J., R.J. Beintema-Hietbrink & G.J.D.M. Müskens 1985. A shift in the timing of breeding in meadow birds. Ardea 73: 83-89.
- Beintema A.J. 1986. Man-made polders in The Netherlands: a traditional habitat for shorebirds. Colonial Waterbirds 9: 196-202.
- Beintema A.J. & G.J.D.M. Müskens 1987. Nesting success of birds breeding in Dutch agricultural grasslands. Journal of Applied Ecology 24: 743-758.
- Beintema A.J. & G.H. Visser 1989. The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77: 181-192.
- Beintema A.J., J.B. Thissen, D. Tensen & G.H. Visser 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. Ardea 79: 31-43.
- Beintema A.J. 1995. Fledging success of wader chicks, estimated from ringing data. Ringing and Migration 16: 129-139.
- Beintema A.J., E. Dunn & D. Stroud 1997. Birds and wet grasslands. In D.J. Pain & M.D. Pienkowski (eds.), Farming and birds in Europe: the Common Agricultural Policy and its implications for bird conservation: 269-296. Academic Press, San Diego.
- Belting S. & H. Belting 1999. Zur Nährungsökologie von Kiebitz- (*Vanellus vanellus*) und Uferschnepfen- (*Limosa limosa*) Küken im wiedervernässten Niedermoor-Grünland am Dümmer. Vogelkundliche Berichte Niedersachsen 31: 11-25.
- Benton T.G., J.A. Vickery & J.D. Wilson 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18: 182-188.
- Berg A. 1992. Factors affecting nest-site choice and reproductive success of Curlews *Numenius arquata* on farmland. Ibis 134: 44-51.
- Birdlife International 2004. Birds in Europe. Population estimates, trends and conservation status. Birdlife International, Wageningen.
- Blake S., G.N. Foster, M.D. Eyre & M.L. Luff 1994. Effects of habitat type and grassland management-practices on the body-size distribution of Carabid beetles. Pedobiologia 38: 502-512.
- Bradbury R.B. & U. Bradter 2004. Habitat associations of Yellow Wagtails *Motacilla flava flavissima* on lowland wet grassland. Ibis 146: 241-246.

- Chamberlain D.E. & R.J. Fuller 2000. Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. Agriculture, Ecosystems & Environment 78: 1-17.
- Devereux C.L., C.U. McKeever, T.G. Benton & M.J. Whittingham 2004. The effect of sward height and drainage on Common Starlings *Sturnus vulgaris* and Northern Lapwings *Vanellus vanellus* foraging in grassland habitats. Ibis 146 (Suppl 2): 115-122.
- Donald P.F., R.E. Green & M.F. Heath 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London Series B 268: 25-29.
- Funke, W. 1971. Food and energy turnover of leaf-eating insects and their influence on primary production. In: H. Ellenberg (ed.) Integrated experimental ecology. Ecological Studies 2: 81-93. Springer, Berlin.
- Gershwin M.E., R.S. Beach & L.S. Hurley 1985. Nutrition and immunity. Academic Press, Orlando.
- Green R.E. 1988. Effects of environmental factors on the timing and success of breeding of Common Snipe *Gallinago gallinago* (Aves, Scolopacidae). Journal of Applied Ecology 25: 79-93.
- Green R.E., G.A. Tyler, T.J. Stowe & A.V. Newton 1997. A simulation model of the effect of mowing of agricultural grassland on the breeding success of the corncrake (*Crex crex*). Journal of Zoology 243: 81-115.
- Guldemond J.A., F. Parmentier & F. Visbeen 1993. Meadow birds, field management and nest protection in a Dutch peat soil area. Wader Study Group Bulletin 70: 42-48.
- Guldemond J.A., M.C. Sosa Romero & P. Terwan 1995. Weidevogels, waterpeilen en nestbescherming: tien jaar onderzoek aan Kievit *Vanellus vanellus*, Grutto *Limosa limosa* en Tureluur *Tringa totanus* in een veenweidegebied. Limosa 68: 89-96.
- Haddad N.M., J. Haarstad & D. Tilman 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia 124: 73-84.
- Hurd L.E. & L.L. Wolf 1974. Stability in relation to nutrient enrichment in arthropod consumers of old-field successional ecosystems. Ecological Monographs 44: 465-482.
- Inouye R.S. & D. Tilman 1995. Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. Ecology 76: 1872-1887.
- Kajak A. 1978. The effect of fertilizers on numbers and biomass of spiders in a meadow. Symposia of the Zoological Society of London 42: 125-129.
- Klaassen M. 1994. Growth and energetics of tern chicks from temperate and polar environments. Auk 111: 525-544.
- Kleijn D., F. Berendse, R. Smit & N. Gilissen 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413: 723-725.
- Klomp H. 1951. Over de achteruitgang van de Kievit, *Vanellus vanellus* L., in Nederland, en gegevens over legmechanisme en eiproductie. Ardea 39: 143-182.
- Kruk M., M.A.W. Noordervliet & W.J. ter Keurs 1996. Hatching dates of waders and mowing dates in intensively exploited grassland areas in different years. Biological Conservation 77: 213-218.
- Kruk M., M.A.W. Noordervliet & W.J. ter Keurs 1997. Survival of black-tailed godwit chicks *Limosa limosa* in intensively exploited grassland areas in The Netherlands. Biological Conservation 80: 127-133.

- Lochmiller R.L., M.R. Vestey & J.C. Boren 1993. Relationship between protein nutritional status and immunocompetence in Northern Bobwhite chicks. Auk 110: 503-510.
- Morris M.G. 1981a. Responses of grassland invertebrates to management by cutting 3. Adverse effects on Auchenorhyncha. Journal of Applied Ecology 18: 107-123.
- Morris M.G. 1981b. Responses of grassland invertebrates to management by cutting 4. Positive responses of Auchenorhyncha. Journal of Applied Ecology 18: 763-771.
- Musters C.J.M., M. Kruk, H.J. de Graaf & W.J. ter Keurs 2001. Breeding birds as a farm product. Conservation Biology 15: 363-369.
- Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146: 579-600.
- Perner J., C. Wytrykush, A. Kahmen, N. Buchmann, I. Egerer, S. Creutzburg, N. Odat, V. Audorff & W.W. Weisser 2005. Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European grasslands. Ecography 28: 429-442.
- Rogers L.E., W.T. Hinds & R.L. Buschbom 1976. General weight vs length relationship for insects. Annals of the Entomological Society of America 69: 387-389.
- Rogers L.E., R.L. Buschbom & C.R. Watson 1977. Length-weight relationships of shrub-steppe invertebrates. Annals of the Entomological Society of America 70: 51-53.
- Schäfer M. & L. Haas 1979. Studies of the effect of mowing on the arthropod fauna of an alpine meadow. Drosera 1: 17-40.
- Schekkerman, H. 1997. Graslandbeheer en groeimogelijkheden voor weidevogelkuikens. IBN-rapport 292, DLO Instituut voor Bos- en Natuuronderzoek, Wageningen.
- Schekkerman H. & G. Müskens 2000. Produceren Grutto‘s *Limosa limosa* in agrarisch grasland voldoende jongen voor een duurzame populatie? Limosa 73: 121-134.
- Schekkerman H. & G.H. Visser 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. Auk 118: 944-957.
- Schekkerman H., W. Teunissen & E. Oosterveld 2005. Broedsucces van grutto’s bij agrarisch mozaïekbeheer in ‘Nederland Gruttoland’. Alterra-rapport 1291, Alterra, Wageningen.
- Siepel H. 1990. The influence of management on food size in the menu of insectivorous animals. Proceedings in Experimental and Applied Entomology, N.E.V. Amsterdam 1: 69-74.
- SOVON 2002. Atlas van de Nederlandse broedvogels 1998-2000. Nationaal Natuurhistorisch Museum Naturalis, Leiden.
- Struwe-Juhl B. 1995. Habitatwahl und Nahrungsökologie von Uferschnepfen-Familien *Limosa limosa* am Höhner See, Schleswig-Holstein. Vogelwelt 116: 61-72.
- Swennen C. 1989. Gull predation upon Eider *Somateria mollissima* ducklings - destruction or elimination of the unfit? Ardea 77: 21-45.
- Teunissen W.A. & L.L. Soldaat 2006. Recente aantalsontwikkeling van weidevogels in Nederland. De Levende Natuur 107: 70-74.
- Thorup O. 2006. Breeding waders in Europe 2000. International Wader Study Group, UK.
- van Paassen A.G. 2006. Vrijwillige weidevogelbescherming in Nederland 1993-2004. De Levende Natuur 107: 104-107.
- van Wingerden W.K.R.E., A.R. van Kreveld & W. Bongers 1992. Analysis of species composition and abundance of grasshoppers (Orthoptera, Acrididae) in natural and fertilized grasslands. Journal of Applied Entomology 113: 138-152.

- Verhulst J., D. Kleijn & F. Berendse 2007. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. Journal of Applied Ecology 44: 70-80.
- Vickery J.A., J.R. Tallowin, R.E. Feber, E.J. Asteraki, P.W. Atkinson, R.J. Fuller & V.K. Brown 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38: 647-664.
- Whittingham M.J. & K.L. Evans 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. Ibis 146 (Suppl. 2): 210-220.
- Wilson J.D., J. Evans, S.J. Browne & J.R. King 1997. Territory distribution and breeding success of Skylarks *Alauda arvensis* on organic and intensive farmland in southern England. Journal of Applied Ecology 34: 1462-1478.
- Witt H. 1986. Bruterfolg von Rotschenkel (*Tringa totanus*), Uferschnepfe (*Limosa limosa*) und Austernfischer (*Haematopus ostralegus*) in intensiv benützten Grünland - Beispiele ‘irrtumlicher’ Nistplatzwahl bei Wiesenvögel. Corax 11: 262-300.

Can ‘mosaic management’ improve breeding success and halt the population decline of Black-tailed Godwits *Limosa limosa* in farmland?

7

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Submitted manuscript

1. Like many farmland birds, the largest European population of the globally near-threatened Black-tailed Godwit *Limosa limosa*, in the Netherlands, has been declining for decades despite conservation measures including agri-environment schemes (AES) in farmland. In a new experimental AES aiming to reverse this decline, collectives of farmers implemented integrated site-level habitat management including spatially coordinated postponed and staggered mowing of fields, refuge strips and active nest protection.

2. We evaluated the effectiveness of 'mosaic management' by measuring godwit breeding success in six experimental sites and paired controls. Productivity was higher in mosaics than in controls due to fewer agricultural nest losses. Chick fledging success was poor in both treatments. Productivity could compensate adult mortality in only one AES site.

3. Although creating chick habitat was a major management goal, availability of tall grass during the fledging period did not differ between treatments, mainly because rainfall delayed mowing in all sites and study years. However, chick survival increased with availability of tall grass among sites. Higher chick survival will thus enhance the positive effect of mosaic management in drier years, but sensitivity to weather represents a weakness of the AES design.

4. Available estimates of productivity in Dutch godwits suggest a strong reduction over the past 20 years and implicate chick survival as the main driver of the decline. Earlier mowing of grasslands is the main causal mechanism, but changes in vegetation structure and composition, and increased predation may also have contributed.

5. Demographic rates like breeding success are useful parameters for evaluating effects of management. 'Mosaic management' increases productivity of Black-tailed Godwits, but does not ensure long-term population viability for this flagship species of wet grassland bird communities. More stringent management prescriptions need to improve both the area and the quality (vegetation structure) of grassland mown late. Concentration in areas with favourable preconditions will facilitate implementing such 'deep' measures and improve their effectiveness by optimising other factors including predation risk.

INTRODUCTION

Throughout Europe, biodiversity is declining in agricultural landscapes (Donald *et al.* 2001, Benton *et al.* 2002, Flade *et al.* 2006) including lowland wet grasslands which form the habitat of a formerly rich and diverse breeding bird community (Beintema *et al.* 1997, Wilson *et al.* 2004). Negative effects of agricultural intensification on the birds' reproductive output are generally considered the main cause of these declines (Vickery *et al.* 2001, Newton 2004). The Netherlands, containing a large expanse of wet grassland devoted to intensive dairy farming, still hold internationally important populations of grassland shorebirds, including 47% of the European population of Black-tailed Godwit *Limosa limosa limosa*, a species listed as globally near-threatened (IUCN 2007). The Dutch population declined from ≥125,000 breeding pairs around 1975 to *c.* 62,000 in 2004, of which 60-75% breed in agricultural grasslands (SOVON 2002, Teunissen & Soldaat 2006). Reduced breeding productivity has been implicated as the main cause of this decline (Kruk *et al.* 1997, Schekkerman & Müskens 2000).

Conservation measures for 'meadowbirds' in The Netherlands have included (1) reserves where biodiversity takes priority over agricultural production (currently *c.* 18,000 ha), (2) Agri-Environment Schemes (AES) reimbursing farmers for less intensive field use (27,000 ha) and for protecting shorebird clutches during farming operations (123,000 ha), and (3) similar nest protection by volunteers and unpaid farmers (*c.* 200,000 ha; Musters *et al.* 2001, van Paassen 2006). In 2005, AES received 87% of the €31 million national budget for meadow bird conservation. Management prescriptions of existing AES focus on postponement of cutting and grazing of individual fields. This reduces destruction of eggs and chicks (Beintema & Müskens 1987, Kruk *et al.* 1997) and increases availability of chick foraging habitat (Schekkerman & Beintema 2007, Chapter 6). As godwit broods actively migrate towards unmown fields, this may also enhance the productivity of pairs breeding in the surroundings. However, most existing studies have failed to show positive effects of AES on shorebird breeding densities (Kleijn *et al.* 2001, Kleijn & van Zuijlen 2004, Verhulst *et al.* 2007). Because effects on breeding productivity were not investigated, the possibility remains that AES lead to more fledged chicks but these settle outside the managed sites. However, it is clear that existing AES have not halted the countrywide decline of Black-tailed Godwit and other grassland birds (Teunissen & Soldaat 2006).

Acknowledging the importance of farmland for godwits and the need for spatially coherent management (Whittingham 2007), Dutch conservation organisations designed a new AES to optimise breeding conditions for Black-tailed Godwits within the constraints of modern dairy farming. In this scheme collectives of farmers coordinate field use at the site level to provide sufficient foraging habitat for chicks and create spatial heterogeneity providing resources for all age classes of godwits (and other meadowbird species) within reachable distance throughout the breeding season (*cf* Benton *et al.* 2003). This 'Mosaic management' was put into practice for three years in six experimental sites to investigate its feasibility and conservation performance.

This study evaluated the effect of mosaic management on breeding output of Black-tailed Godwits. We focused on productivity for three reasons. First, it is this demographic variable that the AES aims to increase. Second, breeding output may respond to management immediately while observing an increase in density within a few years is less likely in a long-lived species like Black-tailed Godwit. Third, productivity provides a direct measure of the contribution of management to the wider population while density effects may be confounded by dispersal in addition to local breeding success. We tested two criteria for the AES to be effective: (1) productivity should be increased by the management, and (2) in AES sites it should at least balance adult mortality so that the population can sustain itself. The required level is approximately 0.6 fledged young per breeding pair (Schekkerman & Müskens 2000). Based on our study and previous productivity estimates, we discuss the outlook for conservation of Black-tailed Godwits in modern farmland.

METHODS

Experimental AES

Mosaic management was established at six lowland wet grassland sites in the Netherlands during 2003-2005. Sites were selected on the basis of willingness to cooperate among farmers and the presence of reasonable numbers of breeding godwits. At each site 6-10 farmers participated in an area of 215-334 (mean 281 ± SD 53) ha. Within most sites, some land was owned by non-participants (9 ± 9%). One site included part of a meadowbird reserve (4%) and two bordered on reserves. Table 7.1 lists practical measures making up the AES, their rationale, and area contracted. Mosaics were designed to offer ≥1 ha of preferred grassland (sward height ≥15-20 cm, Schekkerman & Beintema 2007)

TABLE 7.1. Components of the mosaic management AES with rationale and average proportion of area contracted in the six experimental sites.

Management component	Rationale	%
1st cut postponed until 1 or 8 June	Chick feeding habitat and shelter	11%
1st cut postponed until 15 or 22 June	Chick feeding habitat and shelter	7%
Grazing followed by rest until 15 June	Chick feeding habitat in late spring	4%
Sequentially mowing out strips to feed to cattle in stable	Diverse sward height within field, suitable for foraging adults and chicks	4%
Leaving strips uncut on early-cut fields	Escape havens during mowing; feeding habitat and shelter during brood movements	2%
1st cut in May staggered in 3 tranches separated by >1 week	Allow broods to find unmown grass nearby when field of residence is cut	58%
Grazing	No specific conservation rationale	13%
Flooding grassland, 15 February to 15 April or 15 May	Early-season resting and feeding habitat for adults	1%
Marking and mowing around clutches or placing nest protectors over nests	Avoid agricultural egg losses (due to mowing or trampling)	86%
Reduced driving speed during mowing	More chicks able to escape machines	86%

per godwit brood throughout the chick-rearing period, based on previously observed maximum brood densities (Schekkerman *et al.* 1998). Field use was spatially coordinated to allow all broods to reach suitable grasslands within a few 100 m distance.

General design of godwit studies

Each of the six experimental AES sites was paired with a control site (223 ± SD 118 ha). Selection criteria for control sites were proximity to the AES site (0-5 km, mean 2.2 ± 2.4 km), similarity in landscape, field size and shape and water level, and the presence of >20 godwit pairs. Some control sites included a few fields under other AES contracts. Nest protection was employed on nearly all fields in five AES sites and on about 50% in the sixth, and nearly complete in three, partial in two, and absent in one of the control sites. Average godwit territory densities were 27.5 ± SE 4.5 /km^2 in experimental sites and 19.0 ± 3.7 /km^2 in controls.

Breeding productivity was measured in one year in each AES-control pair, and two site pairs were studied per year. One site pair was studied both in 2004 and 2005; results were averaged where appropriate. In one control site we failed to estimate productivity as volunteers stopped marking clutches in response to the presence of a Red Fox *Vulpes vulpes.* As this was probably unrelated to management, excluding this site will not have biased the results.

Measuring breeding productivity (B, fledged young per breeding pair) is difficult in nidifugous birds like godwits, as broods move around and often remain hidden in vegetation. We combined data on hatching success of the majority of nests in the study area with chick survival in a sample of radio-tagged broods to estimate productivity as:

$$B = U \times [1 + (V \times (1-U))] \times L \times K,$$

where U = probability that a clutch survives to hatching, V = probability that a failed clutch is replaced (0.5, based on Schekkerman & Müskens 2000), L = number of eggs hatched per successful clutch, and K = probability that a chick survives to fledging.

Field methods

Volunteers, farmers and researchers usually located >80% of all godwit nests in the study sites (judged from territory counts), and marked them with sticks at 1-3 m distance. Hatching dates were predicted by egg flotation. Nest survival was monitored through repeated visits at intervals from several days to two weeks. Some volunteers recorded only whether nests were successful (≥1 eggs hatched; eggshell fragments present), but in 63% of 364 successful nests, including all of radio-tagged birds, the number of remaining eggs was recorded and hence, by subtraction from clutch size, the number of chicks hatched.

Chick survival was estimated by radio-tagging one parent or the chicks themselves in 5-20 (11.5 ± 5.2) broods per site. Adult godwits were trapped on the nest during late incubation or on newly hatched young, individually colour-ringed and fitted with small radio transmitters as described in Warnock & Warnock (1993). Transmitters (BD-2, Holohil, Canada /Microtes, Netherlands) weighed 3 g and signals ranged 0.5-1 km on the ground and more in flight. Chicks were tagged at hatching (71% of N=226, usually two chicks per brood of four) or at a later age, with smaller transmitters (LB-2, Holohil/Microtes, 1.0 g) with a signal range of 50-300 m depending on the chicks' position and behaviour.

When godwits are approached by observers, diagnostic alarm calls and behaviour show reliably whether living chicks are present, but it was often impossible to count chicks in the tall grass. However, around the fledging age (*c.* 25 days), the chicks more often leave cover, and they are guarded by a parent until 30-33 days old, allowing to establish the number of fledged young. For the only (of 14) successful tagged parent of which we did not know how many chicks fledged, we used a mean for known broods (1.5, Schekkerman & Müskens 2000).

Tagging parents does not yield insight in the causes of chick deaths, important for interpreting variation in breeding success. Therefore in 2004 and 2005 we tagged the chicks themselves, so that dead chicks could be recovered. In 2004, only chicks were tagged. Although most chicks whose radio signal disappeared before the fledging age were recovered dead, 22% were not, leaving doubt about their fate (dead, tag failure, or moved beyond the search range). In 2005, both a parent and two chicks were tagged in the focal broods. This greatly facilitated determining their fate, as adults could be located from larger distances and their behaviour observed after their chicks' signals were lost. This confirmed that all 49 'missing' chicks had died; their parents stopped alarming before the fledging age, except in one case where a tagless sibling survived. In addition, from the number of tagged and tagless chicks fledged within each brood we ascertained that chick survival was not reduced by tagging (Chapter 8).

Broods were relocated every 1-4 days. The presence of living chicks was deduced from their parents' behaviour or from fluctuations in the strength of chick radio signals, indicating movement. Chicks were recaptured every 4-7 days to check transmitter attachment and weigh them. Missing signals were searched for throughout the study area as well as in woodlots potentially containing predators' haunts up to *c.* 5 km away. We also searched with a metal detector under known nests of Grey Heron *Ardea cinerea* and raptors, up to 10 km distance. Causes of death were deduced from the state and location of chick remains.

The agricultural use of all fields in the study areas was recorded at least weekly. The availability of suitable chick habitat was calculated from these data as:

%(chick grass) =
%(uncut grassland) + 0.7 × %(regrowth) + 0.5 × %(refuge strips + strip mowing).

All these types had swards ≥15-20 cm high; 'regrowth' refers to fields cut or grazed earlier in the spring. Weighting factors reflect the proportion of fields covered by tall grass and its suitability as chick habitat (Schekkerman *et al.* 1998). Uncut grassland made up the majority of 'chick grass' (64 ± 39%).

Statistical analyses

Hatching success was calculated from daily clutch survival probabilities (Aebischer 1999), assuming a total exposure of 25 days. For broods with a tagged parent, chick survival was calculated as number of chicks fledged (day 25) divided by number hatched. Survival of tagged chicks without a tagged parent (2004) was estimated with the Kaplan-Meier estimator (Kaplan & Meier 1958), as several chicks were tagged when ≥1 day old and others lost their tag. Maximum and minimum estimates were made by treating chicks that remained 'missing' as either dead or censored from the day their radio signal was lost. In 2005 we ascertained that all 'missing' chicks died before fledging, but as broods with tagged chicks only may be more likely to move beyond the search range and predation seemed more severe in 2005, this result may not be directly applicable to 2004. However as most missing chicks did probably die, minimum estimates were given five times greater weight than maximum estimates. Standard errors for productivity were obtained by bootstrapping, resampling from the probability distributions for the number of chicks hatched per successful clutch (normal distribution), clutch survival (beta distribution), and chick survival (beta distribution).

The effect of AES management was evaluated by pairwise tests, comparing the availability of brood habitat, clutch survival, chick survival and productivity between experimental and nearby control sites with analysis of variance, using 'site pair' as blocking factor. To take into account differences between sites in precision of productivity estimates, these were weighted by the reciprocal of their coefficient of variation. Relationships between breeding parameters and availability of chick habitat were tested by linear regression of the site estimates on the average proportional area of unmown grassland or 'chick grass' during the main chick period. The latter was defined for each site as running from the date when 25% of all local clutches had hatched to 25 days after the date when 75% had hatched. Median hatching dates differed by up to four weeks between sites.

We calculated an index of chick condition at each capture (2004 and 2005 only) by dividing body mass by the mass predicted at the chick's age from the growth curve reported by Beintema & Visser (1989b). No indices were calculated for chicks <3 days old as the curve underestimates mass at these ages. Condition was compared between AES and control sites in a linear mixed model including chick and site pair as random variables and chick age and management as fixed variables. In a second model with chick and site as random variables, we tested for associations between condition and the area of late-mown grassland.

RESULTS

Agricultural field use

The area of uncut grass and 'chick grass' declined with date, similarly in experimental and control sites (fig. 7.1). Availability of these field types during the main fledging period did not differ between AES sites and controls (uncut 29 ± SE 4% *vs.* 25 ± 5%, $F_{1,5}$=1.01, P=0.36; 'chick grass' 37 ± 4% *vs.* 33 ± 4%, $F_{1,5}$=0.74, P=0.43), and neither did the date on which it fell below 50% (19 *vs.* 18 May, $F_{1,5}$=0.11, P=0.75). The lack of a treatment effect on habitat availability was not caused by farmers ignoring AES prescriptions. Mosaic management was somewhat 'diluted' by fields owned by non-participants and by one AES site including 18% arable land, *vs.* 5% in the control. Second, field use in two control sites was relatively low-intensity, although still within the range of modern farmland.

Most important, in all three study years, rainfall forced farmers to postpone mowing to mid- or late May in both experimental and control sites.

Godwit reproduction

Clutch survival (≥1 egg hatched) ranged between 14% and 87% and was higher in experimental sites than in controls (table 7.2). The difference was caused primarily by larger agricultural losses (to mowing and trampling) in control sites. Predation probability did not differ between treatments. Variation in clutch survival among sites was unrelated to the proportion grassland not yet cut or grazed in the chick period (linear regression, $F_{1,10}$=0.05, P=0.82), possibly due to more intensive nest protection by volunteers and farmers in the AES sites.

The mean number of chicks hatched per successful nest varied from 2.8 to 3.9, but did not differ between AES sites and controls (table 7.2). The mean number of chicks hatched per breeding pair, integrating clutch survival and the number of chicks hatched, was higher in AES sites than in controls (table 7.2).

Survival of chicks to fledging averaged 11% (range 0-23%) and did not differ between AES and control sites (table 7.2). However, chick survival was positively correlated with the availability of uncut fields and 'chick-grass' during the main fledging period (fig. 7.2).

The number of young fledged per breeding pair was almost twice as high under mosaic management as in the control sites (0.28 *vs.* 0.16; table 7.2). In contrast to chick survival, breeding productivity was not significantly correlated with the availability of tall grassland in the fledging period (fig. 7.3), mainly because hatching success varied independently. Breeding output exceeded 0.6 young/pair, required to balance mortality, in only one out of seven estimates in AES sites. It was < 0.4 young/pair in all control sites (fig. 7.3).

Of 205 chicks of which the radio signal was lost before fledging, 22% were never recovered, 11% were found dead by unknown causes, 52% were eaten by predators, 7% were killed during grass harvesting, and 8% died in other ways. Proportions did not

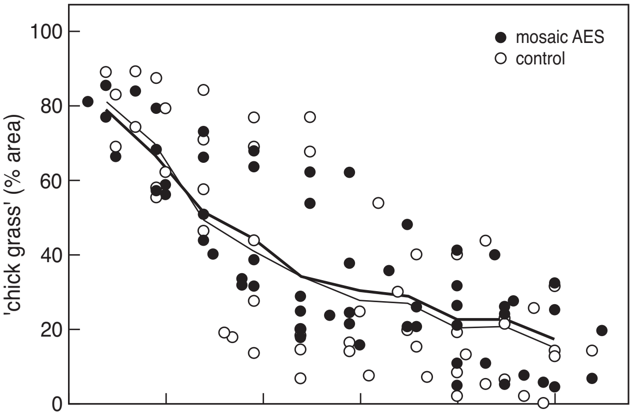


FIGURE 7.1. Availability of 'chick grass' (see methods for definition) in the experimental AES sites (closed dots, bold line) and in control sites (open squares, thin line). Symbols denote actual values, lines treatment averages.

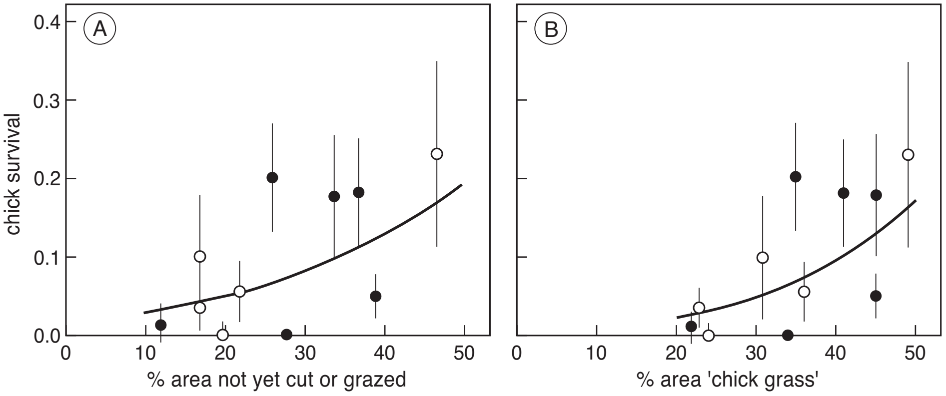
TABLE 7.2. Reproductive parameters of godwits in AES sites and controls. Differences were tested by analysis of variance on site values weighted by (1/cv), but unweighted means are presented here.

Productivity component	mosaic AES		controls		difference		
	mean	SE	mean	SE	F	df	P
clutch survival (U)	0.50	0.03	0.33	0.03	32.7	1,5	0.002
clutch failure, agricultural causes	0.06	0.03	0.29	0.11	6.45	1,5	0.052
clutch failure, predation	0.32	0.08	0.37	0.11	0.58	1,5	0.48
chicks hatched /successful clutch (L)	3.39	0.10	3.22	0.10	1.6	1,5	0.26
chicks hatched /breeding pair	2.09	0.15	1.37	0.15	13.4	1,5	0.015
chick survival to fledging (K)	0.11	0.02	0.11	0.02	0.07	1,4	0.81
chicks fledged /breeding pair (B)	0.28	0.05	0.16	0.05	6.82	1,4	0.059

differ among treatments (χ^2 test, χ^2_4=6.50, P=0.16). Given that most 'missing' chicks must have died (indicated by their tagged parents' behaviour) and may have been transported out of the search range by predators, 'predation' accounted for more than half and up to 80% of chick losses. However, we could usually not distinguish whether chicks had been taken alive or found dead by a predator. Birds (seven species) were identified as chick predators more often than mammals (four species); Common Buzzard *Buteo buteo* (≥9%) and Stoat *Mustela erminea* (≥8%) were identified most frequently.

The average condition index of chicks in 2004 and 2005 was 0.85 (SE=0.01, N=175 measurements on 110 chicks), hence growth rates were lower than reported by Beintema & Visser (1989b) for 1976-1985. Effects of age and management treatment were not

FIGURE 7.2. Survival (± SE) of Black-tailed Godwit chicks to fledging in relation to the availability of uncut grassland and 'chick grass' during the main chick period (black: experimental sites, grey: controls). Lines fitted by logistic regression. A: uncut grassland (logit S = 0.05x -3.93, $F_{1,9}$=4.58, P=0.061); B: 'chick grass' (logit S = 0.07x -5.05, $F_{1,9}$=6.91, P=0.027).



significant (Wald tests, age W_1=2.50, P=0.11, management W=3.43, P=0.06), and chick condition was unrelated to the availability of uncut fields during the fledging period (W_1=0.00, P=0.94).

DISCUSSION

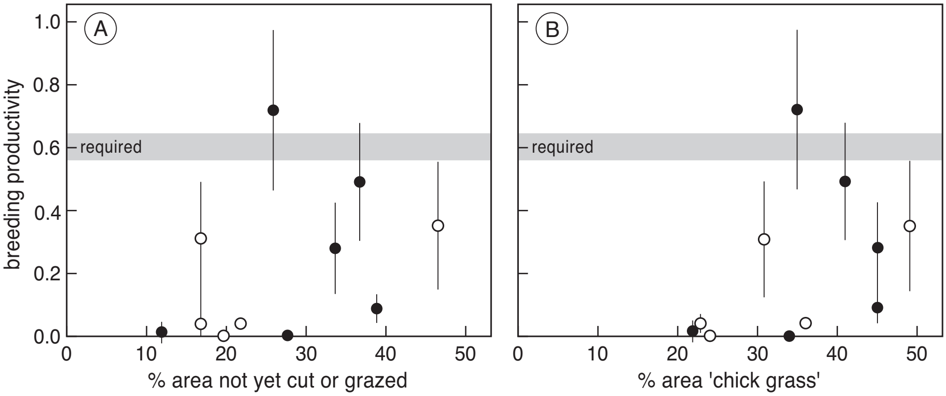
Long-term changes in godwit breeding success

Our study adds significantly to the scant data on Black-tailed Godwit productivity in the Netherlands. The estimates available in the literature were obtained with different methods and in different sites with varying management and therefore do not constitute a true monitoring series, but taken together they indicate that breeding success has declined in the past 20 years (fig 7.4). Although predation has led to very low hatching success in several sites in recent years, clutch survival seems to have declined less generally than chick survival. Due to clutch replacement, it also has a smaller effect on breeding output. In combination with a lack of indication for a poor adult survival (fig. 7.4), this points to reduced chick survival as the main driver of the population decline.

Mosaic management enhances breeding success

Godwit breeding productivity was 75% higher in AES sites than in the paired controls. Although this difference was barely significant in a two-tailed test, based on knowledge of farming practice and godwit biology a higher breeding output was expected in AES sites so that use of a one-sided test is defendable. A weakness in this study was that sites were not selected randomly but using criteria including a positive attitude of

FIGURE 7.3. Productivity (young fledged /breeding pair ± SE) of Black-tailed Godwits in 11 study sites (black: experimental, grey: controls) in relation to the availability of uncut grassland ($F_{1,9}$=1.48, P=0.26) and 'chick grass' ($F_{1,9}$=2.02, P=0.19) during the main chick period. The grey bar indicates productivity required for a stable population. In one site pair we estimated productivity in two years but grassland use was not quantified in the 1st; the 1st year estimates (not shown) were 0.20 ± 0.16 for the mosaic and 0.06 ± 0.05 for the control site.



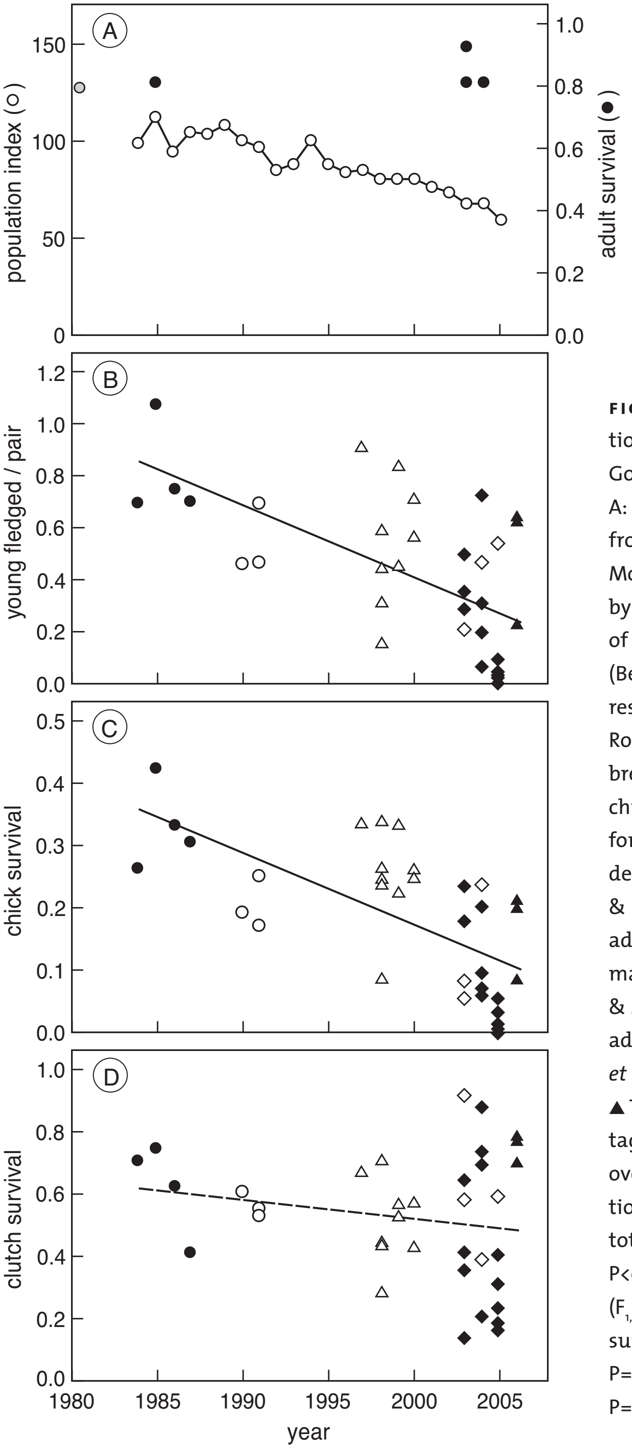


FIGURE 7.4. Changes in population parameters of Black-tailed Godwits in the Netherlands. A: Population indices derived from the SOVON Breeding bird Monitoring Project (dots connected by line), and available estimates of adult survival (◍ ring-recoveries, (Beintema & Drost 1986), ● mark-resighting, (Groen & Hemerik 2002, Roodbergen *et al.* ms). B-D: total breeding productivity (B), and chick (C) and clutch survival (D) for the studies in (B). Symbols denote different studies: ● (Groen & Hemerik 2002), colour-marked adults; ○ (Kruk *et al.* 1997), colour-marked adults; △ (Schekkerman & Müskens 2000), radio-tagged adults; ◆ this study; ◇ (Teunissen *et al.* 2005), radio-tagged chicks ▲ Teunissen *et al.* 2007, radio-tagged adults. The linear trend over time is negative for population index ($F_{1,20}$=113.7, P<0.001), total breeding success ($F_{1,35}$=23.7, P<0.001) and chick survival ($F_{1,35}$=29.0, P<0.001), but not for survival of clutches ($F_{1,35}$=1.43, P=0.24) and adults ($F_{1,4}$=1.69, P=0.26).

farmers towards conservation, and therefore may have been biased towards a positive 'meadowbird history'. This may have led to the higher godwit densities observed in AES sites through local production or immigration. However, reproductive success is sensitive to actual conditions during the breeding period, and much less likely to reflect historical instead of current management than breeding density. We therefore consider our results indicative of a positive effect of mosaic management on godwit productivity.

The higher breeding success in AES sites arose almost entirely through a higher survival of clutches, due to lower agricultural nest losses. The greater intensity of nest protection in the AES sites than in controls probably contributed to this. Nest protection is carried out on *c.* 30% of the agricultural grassland area in the Netherlands (van Paassen 2006), but its nearly complete coverage in the AES sites was part of the management prescriptions.

Previous studies from the Netherlands have shown that differences in meadowbird breeding density between fields managed under AES and controls can be accounted for by differences in groundwater levels rather than any effect of management itself (Kleijn & van Zuijlen 2004, Verhulst *et al.* 2007). However, the higher nest survival found here is unlikely to be related to environmental factors that happen to correlate with fields selected for AES management.

Although mosaic management explicitly aims to increase chick survival, this did not differ between AES sites and controls. A primary objective, making available more 'chick grass' than in conventionally farmed sites, was not achieved. Rainfall forced farmers to postpone mowing in both AES and control sites, and led to a very similar timing of the first cut. It also led to a less spatially diverse grassland use than intended, as cutting was no longer staggered with weekly intervals but proceeded rapidly on fields scheduled for mowing in May when weather improved. Nevertheless, chick survival was positively correlated with the availability of tall grass among sites, irrespective of their treatment status, indicating that mowing later is beneficial to chicks. This suggests that in years with drier May weather, resulting in earlier mowing on conventional farms, better chick survival will add to the higher productivity in AES sites. However, our results do show that mosaic management overlaps with between-year variation in conventional farmland use, and will therefore not deliver value for money in all years, unless prescriptions ensure that mowing is still spread in time and space after an initial postponement.

Mosaic management does not safeguard populations

Average productivity of Black-tailed Godwits in AES sites (0.28 fledged young /pair) was clearly below the *c.* 0.6 required for reproduction to balance mortality. This criterion is based on estimates of 60% first-year post-fledging survival, 85% adult annual survival, and first breeding at two years (Beintema & Drost 1986, Groen & Hemerik 2002). Its magnitude depends particularly on adult survival, which should be as high as 92% for the observed productivity to be sufficient. Annual survival of colour-marked adult godwits in two of our study sites in 2003-2005 was 81% (95% confidence limits 73-87%; Roodbergen *et al.* subm.). It is therefore improbable that mean adult survival in AES sites reached 92% and we conclude that the observed breeding productivity was insufficient to sustain the population.

Our productivity estimates assume that Black-tailed Godwits relay only once after clutch loss (which is generally the case), and that replacements yield as many fledglings as first clutches. While we did not find a decrease in chick survival with date in this study (unpubl. data), clutch survival may decline later in the season (Beintema & Müskens 1987). As more clutches were lost in the control sites, this would reduce productivity slightly more here and thus enlarge the difference between treatments, but it would not affect our conclusion that productivity in AES sites was insufficient. Hence, godwit populations under mosaic management still depend on immigration for their long-term persistence. As our results show that even fewer young fledge in conventional farmland, the necessary recruits should come from meadowbird reserves, but there are too few data to evaluate whether breeding success is sufficient there.

Mechanisms reducing chick survival in farmland

Several factors likely contribute to the observed decline in chick survival. The correlation between fledging success and availability of uncut grassland points to the importance of mowing regimes. Advancement of mowing dates, comprising both an earlier start and a strong increase in the rate at which successive fields are cut, confronts an increasing proportion of chicks with machinery and creates large expanses of homogeneous short swards offering little food and cover.

Deaths by cutting and harvesting made up at least 7% of chick losses in our study, but may have been underestimated. Some chicks may have been scavenged from recently cut fields, and some transmitters may have been destroyed by machinery or buried in silage stacks. Part of the chicks can escape mowing (Kruk *et al.* 1997), but broods then usually move to a nearby uncut field and risks accumulate when fields are cut in rapid succession. Cutting grassland later and spread in time and space will thus reduce mortality.

A detailed analysis of chick mortality in the current study sites and three others found predation hazard over intervals between radio checks to be twice as high when broods stayed in recently cut or grazed fields as in uncut fields (Chapter 8). Short swards thus render chicks vulnerable to (avian) predators. Hence, a scarcity of uncut grassland that forces broods to use cut fields will increase predation losses.

Invertebrates are less abundant in cut than in uncut grassland, leading to a reduction in foraging success of chicks that is large enough to compromise their growth (Schekkerman & Beintema 2007, Chapter 6). Although chicks grew more slowly in our study than observed by Beintema & Visser (1989b) in 1976-1985, we did not find a correlation between chick condition and the availability of tall grass, and only 2% of the recovered chicks evidently starved to death (uninjured, condition index *c.* 0.5). However, chicks with a deteriorating condition may be quickly eliminated by predators (Swennen 1989, Chapter 8).

Earlier mowing dates may not explain the observed decline in chick survival completely. Similar to our study, Schekkerman & Müskens (2000) found that chick survival increased with the area of grassland mown late in nine farmland sites in 1997-2000, yet average survival was notably higher their than in the current study (mean 26%, fig. 7.4) despite a smaller proportion of fields being mown late (11 ± 2% cut after 31 May vs. 21 ± 6% in the current study). This suggests that additional factors are involved.

Between 1990 and 2005, on average 8% of all grasslands in the N and W Netherlands were reseeded annually (Statistics Netherlands), leading to a strong increase in productive grass monocultures at the expense of herb-rich fields. This likely reduced arthropod abundance and diversity (Vickery *et al.* 2001, Atkinson *et al.* 2006, Chapter 6) or the chicks' ability to move and capture prey in the resulting dense vegetations (Butler & Gillings 2004, Wilson *et al.* 2005). The quality of grassland as chick foraging habitat may thus have declined independent of cutting dates.

Poor condition and survival may also result from unfavourable weather (Beintema & Visser 1989a, Schekkerman & Visser 2001). Linear trends over 1976-2005 (data Royal Netherlands Meteorological Institute) suggest a slight increase in mean daily maximum temperature (from 16.1 to 17.3°C), no change in wind speed and an increase in rainfall duration (from 4% to 6% of time), but were not significant due to interannual variability (linear regression, P=0.15-0.34). As warmer weather and increasing rainfall will have opposite effects on chicks it is as yet unclear how climate variation has affected conditions for growth.

Our finding that 50-80% of non-surviving chicks were taken by predators and that Common Buzzard was frequently involved points to the possibility that predation pressure has increased. Since the late 1970s, buzzards have (re)colonised the entire Dutch 'meadowbird landscape' (SOVON 2002), and other raptors have followed. Simultaneously, intensive farming rendered godwit chicks vulnerable to predators by reducing availability of cover and the density of nesting birds that can cooperate to evict predators (Green 1990). The observed frequency of 'predation' could overestimate its importance if it included much scavenging or concerned mainly chicks with already reduced survival prospects. The telemetry data suggest that scavenging was not very common, but we did observe that chicks in poor condition were more prone to disappear. However, the high predation losses are only partly explained by such interaction effects (Chapter 8).

Conservation outlook

Godwit chick survival has been reduced in recent decades by the advancement of mowing dates, which has increased mowing mortality, reduced food availability, and increased vulnerability to predators. At the same time, quality of uncut grasslands as foraging habitat has probably deteriorated and important predators have increased in number. These changes mean that more stringent conservation measures are necessary now than a few decades ago to raise breeding productivity to a level that can sustain the population. Breeding output was higher under mosaic management than in control sites, but chick survival should still be more than doubled to achieve a self-sustaining population. In view of their population declines, many other grassland birds may face similar problems (Donald *et al.* 2001, Teunissen & Soldaat 2006).

Their low productivity indicates that prospects are bleak for maintaining Black-tailed Godwit populations in farmland if no effective conservation measures are put in place. This would mean the loss of a much appreciated component and indicator of farmland biodiversity and a considerable reduction of the population of this globally near-threatened species. Our results indicate that both the proportion grassland mown late and its quality as chick habitat must be improved substantially. AES prescriptions do not include specifications on fertiliser input or floral composition of fields contracted for late mowing. Including such entry criteria will promote an open vegetation structure with abundant insects. It will decrease the flexibility in field use that currently makes the AES attractive to farmers, but conservation will be helped more by 'deep' measures implemented in parts of the farmland than by widespread efforts that are not effective in the long-term. Concentrating conservation efforts in still existing godwit core areas will make it more feasible to implement such far-reaching measures, and will facilitate optimisation (by choice of location or by management) of environmental conditions that may limit their success, including landscape, water levels, disturbance and predation pressure.

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REFERENCES

- Aebischer N.J. 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. Bird Study 46: 22-31.
- Atkinson P.W., R.J. Fuller, J.A. Vickery, G.J. Conway, J.R. Tallowin, R.E.N. Smith, K.A. Haysom, T.C. Ings, E.J. Asteraki & V.K. Brown 2006. Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. Journal of Applied Ecology 42: 932-942.
- Beintema A.J. & N. Drost 1986. Migration of the Black-tailed Godwit. Gerfaut 76: 37-62.
- Beintema A.J. & G.J.D.M. Müskens 1987. Nesting success of birds breeding in Dutch agricultural grasslands. Journal of Applied Ecology 24: 743-758.
- Beintema A.J., E. Dunn & D. Stroud 1997. Birds and wet grasslands. In: D.J. Pain & M.D. Pienkowski (eds.) Farming and birds in Europe: the Common Agricultural Policy and its implications for bird conservation: 269-296. Academic Press, San Diego.
- Beintema A.J. & G.H. Visser 1989a. The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77: 181-192.
- Beintema A.J. & G.H. Visser 1989b. Growth-parameters in chicks of Charadriiform birds. Ardea 77: 169-180.
- Benton T.G., D.M. Bryant, L. Cole & H.Q.P. Crick 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology 39: 673-687.
- Benton T.G., J.A. Vickery & J.D. Wilson 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18: 182-188.
- Butler S.J. & S. Gillings 2004. Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. Ibis 146: 123-130.
- Donald P.F., R.E. Green & M.F. Heath 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London Series B 268: 25-29.
- Flade M., H. Plachter, R. Schmidt, & A. Werner 2006. Nature conservation in agricultural ecosystems. Quelle & Meyer, Wiebelsheim.
- Green R.E., G.J.M. Hirons & J.S. Kirby 1990. The effectiveness of nest defence by Black-tailed Godwits *Limosa limosa*. Ardea 78: 405-413.
- Groen N.M. & L. Hemerik 2002. Reproductive success and survival of Black-tailed Godwits *Limosa limosa* in a declining local population in The Netherlands. Ardea 90: 239-248.
- IUCN 2007. IUCN Red List of threatened species. http: //www.iucnredlist.org/.
- Kaplan E.L. & P. Meier 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53: 457-481.
- Kleijn, D., F. Berendse, R. Smit & N. Gilissen 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413: 723-725.
- Kleijn, D. & G.J.C. van Zuijlen 2004. The conservation effects of meadow bird agreements on farmland in Zeeland, The Netherlands, in the period 1989-1995. Biological Conservation 117: 443-451.

- Kruk M., M.A.W. Noordervliet & W.J. ter Keurs. 1997. Survival of Black-tailed Godwit chicks *Limosa limosa* in intensively exploited grassland areas in The Netherlands. Biological Conservation 80: 127-133.
- Musters C.J.M., M. Kruk, H.J. de Graaf & W.J. ter Keurs. 2001. Breeding birds as a farm product. Conservation Biology 15: 363-369.
- Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146: 579-600.
- van Paassen A.G. 2006. Vrijwillige weidevogelbescherming in Nederland 1993-2004. De Levende Natuur 107: 104-107.
- Roodbergen M., T.C. Klok & H. Schekkerman submitted. Local adult survival and breeding site fidelity of Black-tailed godwits (*Limosa limosa*) in four local populations in the Netherlands in 2002-2005.
- Schekkerman H. & A.J. Beintema 2007. Abundance of invertebrates and foraging success of Black-tailed Godwit (*Limosa limosa*) chicks in relation to agricultural grassland management. Ardea 95: 39-54.
- Schekkerman H. & G. Müskens 2000. Produceren Grutto's *Limosa limosa* in agrarisch grasland voldoende jongen voor een duurzame populatie? Limosa 73: 121-134.
- Schekkerman H., W.A. Teunissen & G.J.D.M. Müskens, 1998. Terreingebruik, mobiliteit en metingen van broedsucces van grutto's in de jongenperiode. IBN-rapport 403, DLO Instituut voor Bos- en Natuuronderzoek, Wageningen.
- Schekkerman H. & G.H. Visser 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. Auk 118:944-957.
- SOVON 2002. Atlas van de Nederlandse broedvogels 1998-2000. Nationaal Natuurhistorisch Museum Naturalis, Leiden.
- Swennen C. 1989. Gull predation upon Eider *Somateria mollissima* ducklings - destruction or elimination of the unfit? Ardea 77: 21-45.
- Teunissen W.A., H. Schekkerman & F. Willems 2005. Predatie bij weidevogels. SOVON-onderzoeksrapport 2005/11, SOVON, Beek-Ubbergen.
- Teunissen W.A. & L.L. Soldaat 2006. Recente aantalsontwikkeling van weidevogels in Nederland. De Levende Natuur 107: 70-74.
- Teunissen W., F. Willems & F. Majoor 2007. Broedsucces van de Grutto in drie gebieden met verbeterd mozaïekbeheer. SOVON-onderzoeksrapport 2007/06, SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Verhulst J., D. Kleijn & F. Berendse 2007. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. Journal of Applied Ecology 44: 70-80.
- Vickery J.A., J.R. Tallowin, R.E. Feber, E.J. Asteraki, P.W. Atkinson, R.J. Fuller & V.K. Brown 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38: 647-664.
- Warnock N. & S.E. Warnock 1993. Attachment of radio-transmitters to sandpipers: review and methods. Wader Study Group Bulletin 70: 28-30.
- Whittingham M.J. 2007. Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? Journal of Applied Ecology 44: 1-5.

- Wilson A.M., M. Ausden & T.P. Milsom 2004. Changes in breeding wader populations on lowland wet grasslands in England and Wales: causes and potential solutions. Ibis 146 (Suppl. 2): 32-40.
- Wilson J.D., M.J.Whittingham & R.B. Bradbury 2005. The management of crop structure: a general approach to reversing the impacts of agricultural intensification on birds? Ibis 147: 453-463.

Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: influence of predation and agriculture

8

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Submitted manuscript

1. Grassland-breeding shorebirds show widespread declines, due to a reduction in breeding productivity following agricultural intensification. However, there is also concern that increasing predation causes further declines or precludes population recovery. Predation may itself be enhanced by agriculture through changes in habitat or food availability, but little is known about the mortality of nidifugous shorebird chicks.

2. We studied mortality by radio-tagging 662 chicks of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* in 15 farmland sites in the Netherlands. Tagging and handling had no effect on condition and survival of godwit chicks, but body condition was reduced by 6-11% in lapwings wearing a tag >3 days.

3. Fledging success was low (0-24%) in both species. Mortality was highest in young chicks but remained considerable until after fledging. 70-85% of all losses were traced to predators (15 species, predominantly birds), at least 5-10% were due to mowing, and 10-20% to other causes including entrapment in ditches and starvation. Chicks staying in fields that were cut before the next radio check were found much more often as mowing victims, and somewhat more often as prey remains, than chicks in fields not cut, indicating that predation includes a limited amount of scavenging.

4. Predation hazard for Godwit chicks was higher in recently cut or grazed fields than in the tall, uncut grasslands they preferred. Predation risk for lapwings was lowest in grazed fields. In godwit chicks poor body condition increased mortality risk, not only from starvation but also from other causes.

5. Predation on godwit chicks was thus enhanced by intensive farming through a decline in availability of cover, augmented by a reduced body condition possibly due to food availability problems. Changes in farming practice may therefore help reduce predation pressure, though the observed interactions explained only part of the high predation rate in godwits and none in lapwings. Predator abundance has increased in Dutch grassland regions, and chick predation has become a factor that should be considered in planning the type and location of conservation measures.

INTRODUCTION

The study of processes affecting reproduction and mortality is important to understand the population dynamics of animals and to identify appropriate conservation strategies for declining species (Green 2002). Most shorebirds (Charadrii) breeding in wet grasslands have shown severe population declines throughout western Europe (Thorup 2006), and a reduction in breeding output has been identified as the main driver of several of these declines (Green 1988, Peach *et al.* 1994, Besbeas *et al.* 2002, Ottvall 2005, Chapter 7). There is broad agreement that reduced breeding productivity is caused primarily by agricultural intensification, leading to an increase in direct clutch and chick mortality and to food availability problems (Beintema *et al.* 1997, Vickery *et al.* 2001, Wilson *et al.* 2004, Schekkerman & Beintema 2007, Chapter 6). However, concerns have also been raised that predation causes population declines or precludes recovery in response to conservation measures (Grant *et al.* 1999, Langgemach & Bellebaum 2005, Bolton *et al.* 2007). A complicating factor in the ensuing discussions about conservation strategies is the possibility that predation eliminates mainly prey with already reduced survival prospects (Swennen 1989) or interacts with agricultural land use (Evans 2004). For instance, changes in farming practice may alter the amount of protective cover or, via effects on food availability, the chicks' risk-taking behaviour and escape response.

Chicks of most shorebird species are precocial and feed themselves. The resulting high energy requirements make them sensitive to foraging conditions (Schekkerman & Visser 2001), while the associated activity and movements may also render them vulnerable to predators and fatal accidents. Because shorebirds often renest after clutch failure but usually not after losing chicks (Cramp 1983), chick survival is a key component of breeding productivity in this group, but the importance of different loss factors is much less well known for chicks than for eggs.

With the development of small radio transmitters that can be attached to chicks, a practical method has become available to investigate fledging success and causes of chick death in precocial bird species. Radio-tagging has been used to study chick mortality in several precocial birds, including ducks (Korschgen *et al.* 1996, Pietz *et al.* 2003), gamebirds (Riley *et al.* 1998, Larson *et al.* 2001), bustards (Combreau *et al.* 2002), and shorebirds (Miller & Knopf 1993, Grant *et al.* 1999, Pearce-Higgins & Yalden 2003, Ratcliffe *et al.* 2005, Bolton *et al.* 2007). A potential drawback of radio-tagging is that the transmitters may affect the chicks' behaviour or physiology and reduce their survival prospects. Thus, it is important to check whether such negative effects affect the outcome of telemetry studies (Kenward *et al.* 1993, Whittingham *et al.* 1999, Grant 2002, Krapu *et al.* 2006).

In this paper we aim to quantify the importance of different mortality factors, including the roles of predation and agricultural management, in the survival of chicks of the two most abundant grassland shorebirds in The Netherlands, Northern Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa*. We describe causes of death, identity of predators and associations between chick mortality and age, agricultural field use and body condition. We also investigated whether radio-tagging and handling chicks affected their growth and survival.

METHODS

Study species and areas

Both species breed primarily in agricultural grasslands in The Netherlands, but their chicks differ in ecology. While Black-tailed Godwit chicks prefer tall, structured swards and feed on invertebrates living in the vegetation, Northern Lapwing chicks frequent short grass, muddy ground and ditch edges, and take invertebrates mainly from the soil surface (Beintema *et al.* 1991). Both species have declined in The Netherlands, godwits much more strongly than lapwings (SOVON 2002, Teunissen & Soldaat 2006).

The data arose from two studies conducted in 2003-2005, one into the effects of predation on meadow bird populations (Teunissen *et al.* 2005, 2006), and the other on the effectiveness of a new agri-environment scheme for improving breeding success of godwits (Chapter 7). Chicks were studied in 15 sites (lapwing 7, godwit 11 sites) scattered through the Netherlands (table 8.1). Godwits were studied in grasslands used for dairy farming; lapwings in both grasslands and sites with mixed arable and dairy farming. One grassland site was managed entirely and one partly as a nature reserve. In four of the godwit study sites, an experimental agri-environment scheme (AES) aimed at improving breeding conditions for Black-tailed Godwits was implemented, with measures including postponed mowing of grass and leaving refuge strips when cutting (Chapter 7). Although some sites in the predation study were selected on the basis of above-average rates of clutch predation, this does not imply that chick predation was also above average, as predation rates on eggs and chicks were not strongly correlated (r_s=0.37 in godwits, 0.44 in lapwings, Teunissen *et al.* 2005).

Radio-tagging and tracking chicks

In total 297 lapwing and 365 Black-tailed Godwits chicks were radio-tagged, 15-53 (godwit) or 22-58 (lapwing) per site and year. Chicks were tagged within a day after hatching (godwit 86%, lapwing 32%) or at older ages. We used small 153 MHz VHF transmitters (type LB-2, Holohil, Canada, assembled by Microtes, Netherlands), weighing 1.0 g and measuring 5×10×3 mm with a 12 cm whip antenna, with a battery life of ≥40 days. Signal range was usually 100-300 m, more in some conditions (≥1 km when up in a raptor nest), and less in others (down to <50 m when in a ditch or burrow). Transmitters were glued to a 1.5×1.5 cm piece of cloth with superglue, and this was attached to the down on the chick's back, just outside the centre of the synsacrum, with latex-based glue retaining some flexibility (Uhu-Creativ, Uhu, Germany). Chicks were recaptured every 4-7 days to check and restore tag attachment, which deteriorated over time due to breakage of down and growth of underlying feathers. Two chicks were tagged in broods of four, one or two in broods of three. All chicks were ringed and bill length and body mass were recorded at each capture. Age at first capture of chicks not ringed at hatching was estimated from bill length (Beintema & Visser 1989). We calculated an index of condition at each capture by dividing the observed body mass by the mass predicted at the chick's age from published growth curves (Beintema & Visser 1989).

Tagged broods were relocated every 1-5 days (median 2 days) using hand-held receivers and antennas. The presence of living chicks was deduced from their parents' alarm behaviour and fluctuations in the strength of their radio signals, indicating movement. Steady signals were followed up to check whether chicks were alive. Missing chicks were searched for throughout the study area and in bushes and woodlots potentially containing predators' haunts up to several km away. Before batteries expired, most study areas were traversed completely on foot to search for weak signals from transmitters in ditches and burrows. We also searched for rings and transmitters with a metal detector under nesting trees in Grey Heron *Ardea cinerea* colonies and some known raptor nests up to 10 km distance.

In 2005, in sites 10-15 only (table 8.1), one of the parents of the tagged godwit chicks was also fitted with a transmitter (Holohil type BD-2). This greatly facilitated assessing the chicks' fate, as the transmitter signals were stronger and adults could still be located and their behaviour observed after their chicks' signals were lost. Adult behaviour reliably shows whether chicks are alive until about a week after fledging (Schekkerman & Müskens 2000).

Cause of death of recovered chicks was deduced from the state and location of the remains. Locations especially were often informative (e.g. in ditch, among recently cut grass, under raptor nest or plucking tree, in stoat burrow), but the state of the carcass and/or the transmitter (condition, bite or plucking marks) also conveyed information (Teunissen *et al.* subm.). Nevertheless, several cases were left as 'unknown', 'eaten by bird', 'not eaten' etcetera. Field notes and photographs of remains were re-examined after the study to standardise interpretation between observers and utilise experience gained. Transmitters found detached without traces of violence were considered to have fallen off a live chick if tag attachment had last been checked >5 days earlier; otherwise they were categorised as 'chick dead or transmitter lost'.

TABLE 8.1. Study sites with general characteristics, study year(s) and species (L=Northern Lapwing, G= Black-tailed Godwit). AES=Agri-environment scheme aimed at improving godwit breeding success. Sites ranged in size from 117 to 493 ha (mean 268 ± SD 110 ha).

Site		Province	Habitat (soil)	Management	Year	Species
1	Arkemheen	Gelderland	grassland (clay/peat)	dairy farming + reserve	2003-4	L,G
2	IJsseldelta	Overijssel	grassland (clay)	dairy farming, maize	2003	L,G
3	Soest	Utrecht	grassland (clay/peat)	dairy farming + maize	2003	L
4	Leende	N-Brabant	mixed farmland (sand)	arable + dairy farming	2004	L
5	Ruinen	Drenthe	mixed farmland (sand)	maize + dairy farming	2004	L
6	Texel	N-Holland	mixed farmland (sand)	arable + dairy farming	2004	L
7	Tijnje	Friesland	grassland (peat)	meadow bird reserve	2005	L,G
8	Gerkesklooster	Friesland	grassland (clay)	dairy farming with AES	2004	G
9	Grijpskerk	Groningen	grassland (clay)	dairy farming	2004	G
10	Oldeboorn A	Friesland	grassland (peat)	dairy farming with AES	2005	G
11	Oldeboorn B	Friesland	grassland (peat)	dairy farming	2005	G
12	Amstelveen	N-Holland	grassland (clay/peat)	dairy farming with AES	2004-5	G
13	Mijdrecht	Utrecht	grassland (clay/peat)	dairy farming	2004-5	G
14	Noordeloos	Z-Holland	grassland (peat)	dairy farming with AES	2005	G
15	Ottoland	Z-Holland	grassland (peat)	dairy farming	2005	G

Locations of radio-tagged broods were recorded on maps. The agricultural status of all fields in the study areas was mapped at least once but usually several times a week (less in sites 6, 8 and 9). Categories were based on crop type (grass/arable), sward height, and whether fields had been cut or grazed (table 8.3).

Survival analysis

Survival curves were derived according to Kaplan & Meier (1958), including staggered entry of chicks ringed at different ages and right-censoring. Observations on tagged chicks could end in several ways: (1) the chick survived until it lost the transmitter or observations were stopped after fledging or at the end of the season (censored, i.e. removed from the sample at this time), (2) the dead chick or its ring were recovered, (3) its transmitter was found and categorised as 'chick dead or transmitter lost', or (4) its signal was lost before the fledging age but neither chick nor transmitter were recovered (i.e. dead, tag failure, or moved beyond the search range). Minimum and maximum estimates of survival were calculated by treating chicks from categories (3) and (4) as dead and censored respectively from the day their signal was lost.

Effects of environmental covariates on mortality of unfledged chicks were explored with proportional hazard models (Cox 1972), using procedure RPHFIT in Genstat (Payne 2005). Models were run for the overall probability of a chick disappearing and for separate competing risks: 'missing' (no remains recovered), predation (total and by bird or mammal separately), agricultural, and other losses. The models assume an unspecified baseline hazard function (similar to the reciprocal of the Kaplan-Meier survival curve) that is modified proportionally by covariates which may vary in time but are assumed constant during the intervals between consecutive localisations of the chick. Covariates examined were site/year (always included to correct for differences in general conditions including landscape and predator abundance), chick age (always included), type of field in which the chick was observed at the start of the interval, agricultural activity on this field during the interval, and chick body condition. Information was not available on all covariates for each interval. For categorical covariates, a category 'unknown' was included to ensure that all intervals contributed to the baseline hazard and models could be fitted. Because this affects the degrees of freedom for the overall test of significance of the covariate, effects were evaluated from the 95% confidence intervals of the ratios between the mortality risk for each level of the covariate and the baseline hazard (hazard ratios; interval including 1 or not).

Analysing associations between mortality and field characteristics was complicated by the fact that broods often moved between fields during the interval between radio checks. Godwit chicks changed field in 59% of 860 intervals; lapwings were more sedentary and moved in 26% of 988 intervals. By selecting intervals lasting ≤2 days for godwits and ≤3 days for lapwings, we minimised the probability that chicks changed field while still retaining most of the data in the analysis (godwits, 55% *vs.* 74% moved in intervals of 0-2 and >2 days, N=716 resp. 144, χ^2_1=17.6, P<0.001; lapwings, 25% resp. 42% moved in 0-3 and >3 days, N=896 resp. 92, χ^2_1=17.6, P<0.001). Body condition indices were used for intervals both following and preceding the measurement.

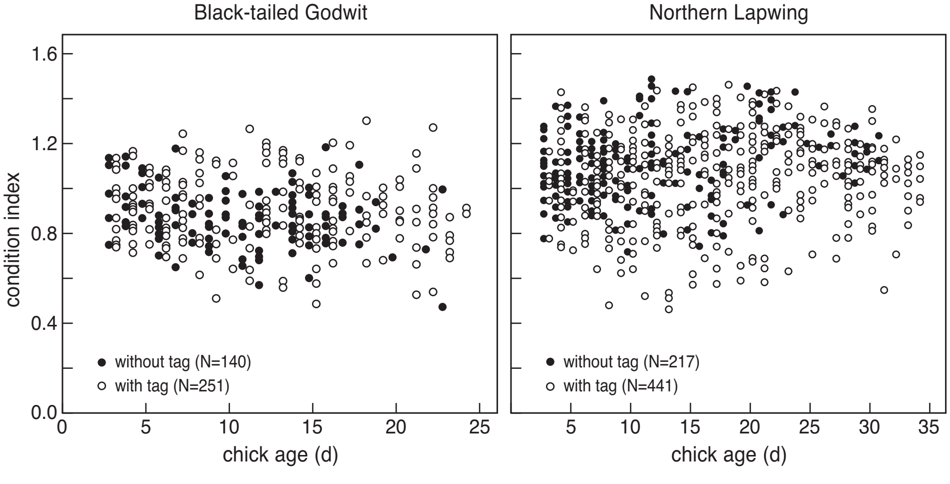
Evaluating effects of radio-tagging

Negative effects of radio-tagging on chicks may arise through entanglement in vegetation (not observed) or by chicks becoming more easily detectable to predators, either because of the transmitters themselves or as a result of handling (scent or behavioural changes). Transmitters may also affect chick growth and condition by hampering feeding or increasing energy expenditure, with possible consequences for risk-taking behaviour and escape response. We checked for such effects in three ways.

We examined the effect of tagging and handling on growth rate using the fact that not all chicks were tagged at the same age. If negative effects occur, the condition index of chicks wearing a transmitter for some time should be less than that of same-age chicks caught for the first time. This was tested in a linear mixed model including site/year and chick ID as random variables (accounting for repeated measures on the same chicks), and chick age and 'days tagged' (tag worn 0, 1-3, or >3 days) as fixed variables. Observations on chicks <3 days old were excluded, as the growth curve underestimates mass of newborn chicks and effects are less likely to show up so early.

Short-term effects of handling on survival were examined by comparing, in a proportional hazard model, mortality over intervals between radio localisations in which chicks were handled (measured and weighed) at the start with that over intervals in which their initial live status was deduced from a distance by the radio signal. Finally, in sites 10-15 in 2005, the survival of tagged godwit chicks (N=127) could be directly compared with that of their tagless siblings (N=100). In these broods half of the chicks and one of their parents were radio-tagged, and both the number of chicks hatched and the number fledged (tagged and total) were known from visual observations made around the fledging age.

FIGURE 8.1. Condition index of chicks in relation to age at first capture (without radio tag) and at later captures (with tag).



RESULTS

Effects of radio-tagging on chicks

In godwit broods with a radio-tagged parent, five of the six chicks surviving to fledging were tagged, and for the sixth this was uncertain (possibly failed tag). Counting this case half in both categories, survival was marginally higher in tagged chicks (GLM with binomial distribution and logit link, $F=4.27$, $P=0.04$). Although the number fledged is small, this does not indicate a lower survival for tagged chicks.

Mortality of godwit chicks over intervals between successive observations was not higher if they were handled and measured at the start of the interval than if they were located from a distance only (hazard ratio $HR=1.05$, $F_1=0.11$, $P=0.74$, $N=685$ handled, 676 non-handled). The same result was obtained in lapwings (hazard ratio 1.08, $F_1=0.20$, $P=0.66$, $N=642$ handled, 734 non-handled).

Condition index of godwit chicks was 0.89 on average ($SD=0.15$, $N=391$) and declined with age (Wald test, $W_1=7.82$, $P=0.005$; fig. 8.1a), indicating a lower growth rate than observed 25 years ago by Beintema & Visser (1989). Tagging and handling did not depress growth rate in godwit chicks: including the variable 'days tagged' (0, 1-3, or >3 days) did not significantly improve the model fit ($W_2=1.16$, $P=0.56$, interaction age.'days tagged' $W_2=4.62$, $P=0.10$). In lapwings, condition indices were higher on average (1.06 ± 0.19, $N=658$) and did not decline with age ($W_1=1.95$, $P=0.16$; fig. 8.1b), but 'days tagged' had a significant effect that increased with age ($W_2=35.7$, $P<0.001$, interaction 'days tagged' × age $W_2=7.97$, $P=0.019$). Lapwings that had worn a tag for >3 days were 6% lighter than tagless chicks when 5 days old, increasing to 11% at 30 days old ($P<0.001$). Chicks tagged for 1-3 days did not differ in condition from tagless chicks ($P=0.37$).

Overall survival and age

The fate of 23% of all radio-tagged chicks remained uncertain as no remains were found, and in a further 3% we were unsure whether chicks lost their transmitter or died (table 8.2). Observations on godwit broods with a tagged parent in 2005 (sites 10-15) showed that all 49 chicks that remained 'missing' had actually died; the parents stopped alarming before they were 25 days old, except in one case where a tagless sibling fledged. Hence true survival was very likely closer to the minimum than to the maximum estimates.

Survival to fledging was low in both species (fig. 8.2). The minimum estimate varied between sites/years from 0 to 24% in godwits (mean 7%, $SD=7\%$, $N=14$ sites), and from 0 to 23% in lapwings (mean 14%, $SD=8\%$, $N=8$). In both species, survival was especially low in 2005 (mean 3% and 4% respectively). Mortality was highest in the first days after hatching, then more or less stabilised before a further decrease around the fledging age (fig. 8.2). Appreciable mortality still occurred after fledging, particularly in lapwing chicks. The initial phase of high mortality lasted longer and encompassed a larger proportion of the total losses in lapwings than in godwits.

Causes of death

Of all chicks lost before fledging (dead or 'missing'), the cause of death remained unknown in 38%, 47% were found eaten by predators, 5% as victims of agricultural activities, and 9% succumbed to other causes (table 8.2). As part of the 'missing' chicks were probably removed by predators (see discussion), predation (including scavenging) was the primary cause of mortality.

Predation hazard declined with chick age by 7% per day (proportional hazard model, godwits F_1=10.9, P<0.001, lapwings F_1=16.6, P<0.001). Birds were more often identified as chick predators than mammals, particularly of lapwings (table 8.2). The four species most frequently identified were Grey Heron (18% of 255 chicks found predated), Stoat/Weasel *Mustela erminea/nivalis* (15%), Common Buzzard *Buteo buteo* (12%), and Carrion Crow *Corvus corone* (6%); 11 other species made up ≤2% each (White Stork *Ciconia ciconia*, Goshawk *Accipiter gentilis*, Sparrowhawk *A. nisus*, Marsh Harrier *Circus aeruginosus*, Common Kestrel *Falco tinnunculus*, Jackdaw *Corvus monedula*, Lesser Black-backed Gull *Larus graelsii*, Common Gull *L. canus*, rat *Rattus sp.*, Domestic Cat *Felis catus* and Red Fox *Vulpes vulpes*). While lapwing chicks were taken more often by herons than godwits (11% *vs.* 26%, χ^2_1=7.90, P=0.005), godwit chicks were taken more by stoats (8% *vs.* 20%, χ^2_1=5.49, P=0.02) and buzzards (6% *vs.* 17%, χ^2_1=6.30, P=0.01), and both species equally by crows (6% *vs.* 7%, χ^2_1=0.11, P=0.74). Godwit chicks prefer tall vegetations (94% of 1036 localisations in fields with uncut or regrowing sward >15-20 cm high *vs.* 37% of 1186 in lapwings) where they were proportionally more often taken by mammals (mostly Stoats) than in short swards (43% *vs.* 20% of predations by mammals, χ^2_1=4.62, P=0.032; table 8.3).

TABLE 8.2. Summary of fates and causes of death of radio-tagged chicks, pooled over study sites and years. 'Difference' gives χ^2-test of differences in prevalence between godwits and lapwings.

Fate	Total		Godwit		Lapwing		Difference	
Number of chicks tagged	662		365		297			
survived observation period	119	18%	49	13%	70	24%		
loose transmitter: lost or dead	23	3%	6	2%	17	6%		
missing, no remains found	150	23%	83	23%	67	23%		
dead, transmitter or chick found	370	56%	227	62%	143	48%		
Causes of death (% of lost chicks)	543		316		227		χ^2_1	P
'missing' + 'transmitter lost or dead'	173	32%	89	28%	84	37%	3.24	0.072
dead, cause unknown	35	6%	28	9%	7	3%	6.84	0.009
eaten by bird	155	29%	83	26%	72	32%	1.38	0.24
eaten by mammal	65	12%	50	16%	15	7%	9.37	0.002
eaten, predator unknown	35	6%	16	5%	19	8%	2.24	0.13
agricultural activity & trampling	26	5%	22	7%	4	2%	7.46	0.006
drowned/stuck in ditch/trench	29	5%	15	5%	14	6%	0.50	0.48
starvation / illness	13	2%	9	3%	4	2%	0.65	0.42
other causes	11	2%	4	1%	7	3%	2.16	0.14

All agricultural losses concerned chicks killed during mowing and harvesting of grass, except for one newborn lapwing trampled by cattle. More godwit than lapwing chicks fell victim to mowing (table 8.2), due to the godwits' preference to forage in tall grassland ready to be mown. In godwit chicks the risk of mortality by mowing tended to decline with age (-10% /day, F_1=3.60, P=0.058) although chicks up to 23 days old were killed by machines. Too few lapwings were killed by mowing to find an age effect.

About 5% of lost chicks died in wet (both species) or dry (lapwing only) ditches. Although chicks swim well, ditches can form a trap when the sides are too steep to climb. Risk of entrapment in ditches declined with age in lapwings (-17% /day, F_1=14.1, P<0.001), but not significantly in godwits (-10% /day, F_1=2.17, P=0.14). Other causes of death included starvation or illness (2%), acute exposure to cold or rain (1%), and aggression by conspecifics (1 case).

Mortality and field use

Relative to the most-used field type (uncut grassland), the risk that godwit chicks were taken by a predator was twice as high in recently cut or grazed fields with a short sward (table 8.3). This effect was caused by avian predators, and translated into a 1.4 times higher overall mortality. The risk of predation by mammals was especially high in previously cut fields with a regrowing sward, but as mammal predation was less frequent this did not translate into a higher overall mortality. The only significant effect of field type on mortality of lapwing chicks was a lower risk of predation (by birds) in grazed fields. Predation hazard for godwits was also low here, but not significantly different from uncut grassland (table 8.3).

Godwit chicks located in fields with a tall (uncut or regrowing) sward were 13 times more likely to be found as a mowing victim when the field was cut during the subsequent interval than when it was not, but the associated 50% increase in overall mortality was not significant (table 8.3). No lapwing chicks were killed by mowing in intervals ≤3 days. Because avian predators and scavengers are often attracted to mowing activity, it is of interest whether other risks increased when the field was cut. Hazard ratios for predation (particularly by birds) were greater than 1, but the effect was not significant (godwit P=0.15, lapwing P=0.10). It was significant in godwits when only 1-day intervals were considered (HR=22, P=0.07). The probability that chicks went 'missing' was not associated with cutting of the field (table 8.3).

Mortality and condition

A low body condition index greatly increased the risk of dying by 'starvation or illness' in both species (table 8.4), which is expected as the diagnosis was based on a lack of injuries combined with a poor condition. The mean condition index of chicks considered to have died from starvation was 0.48 (SD=0.06, range 0.41-0.56, N=10). In godwits but not in lapwings, condition affected the overall risk of mortality, and there was also a near-significant tendency for godwit chicks in poor condition to be lost to causes other than starvation or illness. This was not so much due to predation (except by mammals) as to a higher probability to end up 'missing' (table 8.4). In lapwings no condition effects were observed on risks other than starvation.

TABLE 8.3. Proportional hazard analysis for different causes of death, in relation to the field type where chicks stayed at the start of observation intervals, and (for chicks in uncut or regrowing grassland) to whether the field was cut during the interval. Hazard ratios (HR) are given relative to the site- and age-specific mortality risk in uncut grasslands (baseline hazard), with 95% confidence limits. Ratios significantly different from 1 are printed in bold ($^{+}$=P<0.10, *=P<0.05, **=P<0.01). N is the total number of intervals (≤2 days in godwits, ≤3 days in lapwings) for each type. Description of field types given below table.

Field Type	N	Lost (dead/ missing)		Predation total		Predation by birds		Predation by mammals		'Missing' (not recovered)		Mowing & trampling	
		HR	95%CI	HR	95%CI	HR	95%CI	HR	95%CI	HR	95%CI	HR	95%CI
Black-tailed godwit													
Uncut grass[1]	638	1.0		1.0		1.0		1.0		1.0		1.0	
Regrowing grass[2]	70	1.1	0.6–2.2	1.9	0.6–5.7	0.5	0.0–4.2	**5.2***	**1.2–23.8**	0.7	0.2–2.5	0.4	0.0–4.3
Refuge strips[3]	36	2.0^{+}	1.0–4.1	1.9	0.7–5.4	1.0	0.3–3.4	0.0	0– >100	1.4	0.3–6.5	9.7^{+}	0.7–122
Grazed grass[4]	105	0.7	0.4–1.3	0.6	0.2–1.8	0.8	0.2–2.8	0.6	0.1–4.5	1.1	0.5–2.2	0.0	0– >100
Short grass[5]	135	1.4^{+}	0.9–2.2	**2.0***	**1.1–3.7**	**3.2****	**1.5–6.7**	1.0	0.3–3.4	1.1	0.6–2.4	0.0	0– >100
In uncut & regrowing grass:													
field not cut in interval	601	1.0		1.0		1.0		1.0		1.0		1.0	
field cut in interval	46	1.5	0.8–2.8	1.8	0.6–5.6	2.8	0.7–11.0	1.3	0.1–13.8	0.8	0.2–2.6	**13.4****	**3.2–56**
Northern lapwing													
Uncut grass[1]	175	1.0		1.0		1.0		1.0		1.0			no fit
Regrowing grass[2]	303	0.9	0.4–1.6	0.7	0.3–1.6	1.0	0.3–3.0	0.1^{+}	0.0–1.3	1.6	0.5–5.1	-	-
Grazed grass[4]	349	**0.5***	**0.3–0.9**	**0.2****	**0.1–0.6**	**0.2***	**0.1–0.7**	0.5	0.1–3.1	1.4	0.5–4.3	-	-
Short grass[5]	87	1.1	0.5–2.4	0.8	0.3–2.8	2.1	0.5–9.7	0.0	0– >100	2.7	0.8–9.0	-	-
Arable[6]	104	0.9	0.4–2.3	0.3	0.1–1.3	0.7	0.1–4.5	0.1	0.0–2.9	3.0	0.7–12.6	-	-
In uncut & regrowing grass:													
field not cut in interval	450	1.0		1.0		1.0		1.0		1.0		-	-
field cut in interval	28	1.1	0.3–3.8	1.6	0.3–8.3	4.6^{+}	0.8–27.8	0.1	0– >100	1.4	0.2–12.9	-	-

1 Grassland not yet cut or grazed in the present year, vegetation usually ≥15-20 cm high. 2 Grassland previously cut or grazed, vegetation regrown to ≥15-20 cm. 3 Recently (≤3 weeks ago) cut grassland with strips of tall vegetation (usually 2-10 m wide) left uncut. 4 Currently grazed grassland, vegetation height dependent on time grazed. 5 Recently cut or grazed grassland where regrowing vegetation has not yet reached 15-20 cm. 6 Diverse arable crops including maize fields within grassland areas.

DISCUSSION

Radio-tagging as a method to study mortality of shorebird chicks

Our study did not reveal negative effects of radio-tagging and handling on condition and survival of Black-tailed Godwit chicks. Northern Lapwing chicks that had worn a tag longer than 3 days were 6-11% lighter than same-age chicks captured for the first time. This suggests that tags induced negative effects on growth, by reducing the chicks' insulation, increasing energy costs of locomotion or impairing foraging success. Lapwing chicks are smaller than godwits and therefore the transmitter adds proportionally more to their body mass (5.7% *vs.* 3.5% at hatching, decreasing to 0.5% at fledging), which may help explain why we did not observe a condition effect in godwits. We found no association between condition and the overall survival of lapwing chicks (table 8.4), but condition indices ≤0.6, associated with a strongly increased risk to be found starved, were only observed in tagged lapwings (fig. 8.1). Since no adult lapwings were radio-tagged we could not directly compare the survival of tagged chicks with that of tagless siblings, like in the godwits, but a study in the UK did observe that poor condition induced by repeated handling reduced survival of lapwing chicks (F. Sharpe *et al.* unpubl.). Other studies generally did not find adverse effects of back- or leg-mounted tags in chicks of shorebirds and gamebirds (Kenward *et al.* 1993, Whittingham *et al.* 1999, Grant 2002). Nevertheless, there may be effects of telemetry studies that cannot be detected by within-brood comparisons. For instance, effects of repeated disturbance during tracking of broods will affect both tagged and tagless chicks equally.

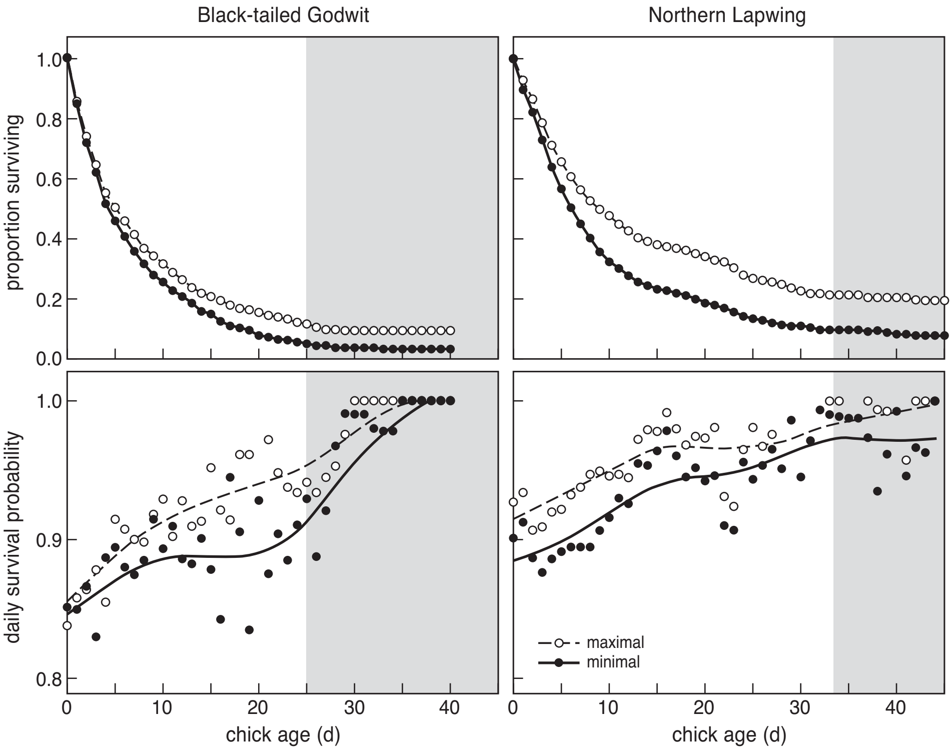
Notwithstanding these potential problems, radio-tagging provides the only feasible method to study causes of death of chicks. In our study, 6-9% of observed deaths could not be attributed to a cause, and 23% of all chicks disappeared without a trace. The contribution of different mortality factors may well differ between 'missing' chicks and those found dead. Indeed it is even uncertain whether 'missing' chicks died or

TABLE 8.4. Hazard ratios for different causes of death, for a reduction in the body condition index of chicks from 1 (baseline hazard) to 0.6 (a very poor condition, fig. 8.1). Hazard ratios (HR) are given with 95% confidence limits and P-values indicating whether they differ significantly from 1. Models for agricultural losses did not converge.

Hazard type	Black-tailed Godwit (N=554)			Northern Lapwing (N=825)		
	HR	95% CI	P	HR	95% CI	P
All mortality (dead and missing)	3.0	1.6–5.6	<0.01	1.1	0.7–1.6	0.67
All except starvation/illness	1.9	1.0–3.8	0.06	1.0	0.7–1.5	0.99
Predation (total)	1.0	0.4–2.7	0.99	0.9	0.5–1.7	0.86
Predation (bird)	0.8	0.2–3.5	0.82	0.7	0.3–1.5	0.40
Predation (mammal)	2.7	0.4–16.0	0.29	1.4	0.2–8.1	0.70
'Missing'	2.1	0.7–6.2	0.17	0.8	0.5–1.5	0.56
Other (including starvation)	219.6	12.5–3872	<0.01	20.5	3.6–116	<0.01

survived with a failed tag or after moving out of the search area. The resulting minimum and maximum estimates of chick survival lay so far apart (fig. 8.2) that estimating reproductive success from tagging chicks would be problematic without additional information. In the Black-tailed Godwits and in Eurasian Curlews *Numenius arquata* studied by (Grant 2002), the additional tagging of one parent greatly enhanced the interpretation of the chicks' fate and the precision of survival estimates. None of the 'missing' chicks of tagged godwits survived to fledging. As tagged parents are easier to relocate than tagged chicks and as mortality seemed especially high in 2005, this result may not hold for all missing chicks, but it is very likely that most signal losses reflected chick deaths. Transmitters may have been destroyed by mowing and harvesting machinery or buried in silage stacks (signals lost when buried >1.5 m deep, unpubl.

FIGURE 8.2. Survival curves (upper panels) and daily survival rates (lower panels, with smoothing splines, df=4) of Black-tailed Godwit and Northern Lapwing chicks, pooled over sites and years. Maximum and minimum estimates are based on different assumptions about the fate of 'missing' chicks; minimum values are more likely to be true. Grey areas indicate ages at which chicks had fledged. Godwit sample size varied from 298 chicks at hatching to 39 at fledging and 9 on day 40 (3526 chick days in total); lapwing sample size from 66 at hatching to 131 on day 4, 51 at fledging and 18 on day 45 (3349 chick days in total).



obs.), but as the probability that a chick ended up ‘missing’ was not higher if the field in which it stayed was cut during the observation interval, this is unlikely to have occurred frequently. Some signals may have been lost when chicks drowned, but as most ditches in our study areas were shallow this was probably not a major cause either. Probably, most ‘missing’ transmitters were destroyed by predators or carried out of the search range to distant sites or deep burrows.

In bird species where parents stay with the brood until fledging, we recommend tagging both chicks and parents to study details of chick mortality including causes of death. If the primary aim is to quantify breeding success or brood movements, we prefer tagging parents only as it makes tracking less time-consuming and minimises negative effects on chicks.

Identifying predators

No less than 15 species were identified as chick predators in this study, with common Buzzard, Grey Heron and Stoat/Weasel recorded most frequently. The large fraction of unidentified causes of death calls for caution in interpreting the importance of different species, as some may leave more readily identifiable remains than others. Red Foxes might be particularly likely to bury or destroy transmitters, but in two of our study sites where foxes were known to be absent neither the fraction lost to unknown causes (30% *vs.* 39%, χ^2_1=0.92, P=0.34) nor the share of mammals in known predations (41% *vs.* 26%, χ^2_1=2.61, P=0.11) were lower than in the eight sites where foxes were present. This makes it unlikely that foxes were responsible for the majority of unexplained losses. Stoats and Weasels also bury chicks underground (often in European Mole *Talpa europaea* tunnels), but in several cases where we located such caches we could pick up the signals from distances up to 50-100 m. Nevertheless, buried tags are less easily located than tags under raptor nests or plucking trees and we may have missed those buried deep. However, such bias would have to be strong to fully explain the large share of avian predators in chick predation. This contrasts with predation on shorebird eggs, where mammals, particularly Red Fox, usually take a larger share (Langgemach & Bellebaum 2005, Bolton *et al.* 2007, Teunissen *et al.* 2006, subm.).

The greater contribution of Stoat and smaller share of Grey Heron in predation of godwit than lapwing chicks (table 8.3) is probably associated with vegetation preferences. Stoats do not usually hunt and are less likely to approach chicks unnoticed in the short (cut and grazed) swards preferred by lapwing chicks, but herons often forage in short (cut) grassland swards (unpubl. obs.).

Disentangling the roles of predation and agriculture

Chick survival rates observed in this study are low compared to previously published estimates, both for Black-tailed Godwits (7% *vs.* 9-46%; Beintema 1995, Ratcliffe *et al.* 2005, Chapter 7) and Northern Lapwings (14% *vs.* 7-50%; Galbraith 1988, Baines 1990, Beintema 1995). Predation was the most frequent direct cause of death; we estimate that 70-85% of all lost chicks were taken by predators, 5-10% were mowing victims, and 10-20% died of other causes. However, mowing losses may have been underrecorded, as in 2004 the first grass cut was already underway in some sites before we tagged most chicks. Also, in the four godwit AES sites, grassland use included measures aimed at avoiding chick losses. Mowing losses tended to be lower in AES sites than in controls, but the difference was not significant (5% *vs.* 11%, Chapter 7). Finally, mowing victims may have been removed by scavengers, and as we could rarely deduce this from the remains, these would have been recorded as predated. Avian predators regularly foraged among the cut grass on recently mown fields. If many dead or injured chicks were taken here, not only a chick's probability to be found as a mowing victim, but also its probability to be found 'predated' should be higher if its field of residence was cut during the interval between observations than if it was not. Although predation hazard ratios tended to be greater than 1 if the field was cut, the effect was significant only for one-day intervals in godwits. Scavenging probably occurs mainly on the first day after mowing and its effect may be diluted by 'true' predation over longer observation intervals. Although some chicks may thus have been removed from cut fields by predators, their number was probably smaller than that of identified mowing victims, otherwise a clearer effect on predation hazard would be expected.

Predation may be enhanced by farming practice through changes in vulnerability of prey to predators. Godwit chicks were 2-3 times more likely to be killed by a (avian) predator if they stayed in recently cut or grazed fields than in uncut grasslands, which form their preferred habitat (table 8.3, Chapter 6). The small chicks are less visible here, while detection of predators is taken care of by the larger parents. Hence, godwit broods that are forced to forage in or frequently travel through cut fields due to a scarcity of uncut grassland are more likely to suffer predation losses. By multiplying the observed average daily survival rate with the field-type specific hazard ratio divided by the average of the hazard ratios for all field types weighted according to their frequency of use (table 8.3), 2.7% of chicks instead of the observed 7.2% are predicted to fledge if broods had to stay in short-sward grasslands throughout. Survival would increase to 8.7% if broods stayed in uncut fields continuously. Field use can thus induce a more than threefold change in predation rate, but this interaction effect does not explain why godwit chicks survived poorly in all field types in our study. Nevertheless, overall survival of Black-tailed Godwit chicks increases with the availability of tall (not cut or grazed or sufficiently regrown) grassland swards during their prefledging period (Schekkerman & Müskens 2000, Chapter 7).

Predation on lapwing chicks was not reduced on uncut fields. Their earlier hatch dates, (causing fields to have shorter swards when visited by lapwings than by godwits) and the fact that within uncut fields lapwing chicks will feed in patches with less vegetation may contribute to this. Lapwings prefer short swards, including grazed fields where they ran a significantly lower predation risk that was also observed (but not significant) in godwits. Possibly, some predator species including Grey Herons and Stoats avoid to hunt in fields with livestock.

The importance of predation may be overestimated if it selectively affects individuals with already reduced survival prospects (e.g. Swennen 1989). Might predation represent the final elimination of shorebird chicks that lag behind in growth because of suboptimal feeding conditions? Godwit growth in our study was retarded in comparison to measurements from the 1980s (Beintema & Visser 1989), and this may reflect a deteriorated food supply due to agricultural intensification (Schekkerman & Beintema 2007, Chapter 6). In both godwit and lapwing chicks the likelihood to be found starved increased with declining body condition, but other hazards increased only in godwit chicks, where the probability to end up ‘missing’ was elevated rather than that of predation. This is unexpected given our interpretation that most ‘missing’ chicks were depredated. Modifying daily survival rates by the estimated hazard ratio predicts that average chick survival would increase to just 11% in godwits at a mean body condition of 1 instead of the observed 0.89. In lapwing chicks, condition had no significant effect on deaths other than by starvation, and did not affect overall mortality rate. This suggests that predators did not strongly select chicks in poor condition, but it cannot be excluded that chicks experiencing food shortage extend their foraging activity or take more risks and are eliminated even before their condition is visibly affected. A poor condition did increase predation on lapwing chicks in a similar study in the UK (Sharpe *et al.* unpubl.).

Conservation implications

Our results indicate that predation on Black-tailed Godwit chicks is increased up to three times by intensive agricultural grassland use through a reduced availability of fields with protective cover, and possibly also by a reduction of food availability leading to poor body condition or risky foraging behaviour. Cutting fewer grasslands early will therefore reduce predation losses in addition to direct losses due to mowing and starvation. However, these interactions between predation and agriculture explained only part of the high predation rate observed in godwits and none in Northern Lapwings. Some frequent chick predators have increased notably in the wet grassland regions of The Netherlands. Common Buzzards were absent here until the 1980s, but now occur nearly everywhere (SOVON 2002). Goshawk, Sparrowhawk, White Stork, Carrion Crow, gulls and Red Fox have also increased. This partly represents a return to natural population levels after historical reduction by human persecution and pollution, but is greatly enhanced by man-made changes opening up formerly unsuitable landscapes to several of these species. Though Grey Heron has been common throughout and Stoat and Weasel have declined, overall predator abundance has probably increased. Simultaneously changes in farming practice made grassland birds more vulnerable to predation, through the interactions described here and by reducing via breeding density the ability of meadowbirds to cooperatively evict potential predators (Green *et al.* 1990). Over the past 20 years, prefledging survival of Black-tailed Godwit chicks has declined significantly in the Netherlands (Chapter 7). There are very few historical data on mortality of lapwing chicks, which are less sensitive to changes in grassland cutting regimes. Between 1990 and 2000 Northern Lapwings declined less rapidly in The Netherlands than Black-tailed Godwits (-0.5 *vs* -1.9% per year), but since 2000 the population has shown an annual 3.4% decline that approaches that of godwits (-5.6%; Teunissen 2007). It is possible that the recent acceleration in the declines of both species shows the additive effect of increased predation on top of that of ongoing agricultural intensification.

An increasing predation pressure makes conservation measures to counteract negative effects of modern farming even more urgent than before. ‘Shallow’ measures that worked 30 years ago may no longer suffice to raise meadowbird breeding productivity to a level that can sustain the population. Control of predation is a complex matter scientifically, ethically, and practically, and requires careful consideration of all available options (Bolton *et al.* 2007). There is much to gain by considering effects on predation risk in the development of practical conservation measures, and in concentrating these in areas with optimal external preconditions, including a landscape structure that does not sustain high predator densities, or in areas where such conditions can be created.

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REFERENCES

- Baines D. 1990. The roles of predation, food and agricultural practice in determining the breeding success of the Lapwing (*Vanellus vanellus*) on upland grasslands. Journal of Animal Ecology 59: 915-929.
- Beintema A.J. & Visser G.H. 1989. Growth-parameters in chicks of Charadriiform birds. Ardea 77: 169-180.
- Beintema A.J., J.B. Thissen, D. Tensen & G.H. Visser 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. Ardea 79: 31-43.
- Beintema A.J. 1995. Fledging success of wader chicks, estimated from ringing data. Ringing and Migration 16: 129-139.
- Beintema A.J., E. Dunn & D. Stroud 1997. Birds and wet grasslands. In: D.J. Pain & M.D. Pienkowski (eds.) Farming and birds in Europe: the Common Agricultural Policy and its implications for bird conservation: 269-296. Academic Press, San Diego.
- Besbeas P., S.N. Freeman, B.J.T. Morgan & E.A. Catchpole 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58: 540-547.
- Bolton M., G. Tyler, K. Smith & R. Bamford 2007. The impact of predator control on Lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. Journal of Applied Ecology 44: 534-544.
- Combreau O., J. Qiao, M. Lawrence, X. Gao, J. Yao, W. Yang & F. Launay 2002. Breeding success in a Houbara Bustard *Chlamydotis undulata macqueenii* population on the eastern fringe of the Jungar Basin, People's Republic of China. Ibis 144: E45-E56.
- Cox D.R. 1972. Regression models and life tables. Journal of the Royal Statistical Society, series B 34: 187-220.
- Cramp S. (Ed.) 1983. The birds of the western Palearctic 3. Oxord University Press, Oxford.
- Evans K.L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146: 1-13.
- Galbraith H. 1988. Effects of agriculture on the breeding ecology of Lapwings *Vanellus vanellus*. Journal of Applied Ecology 25: 487-503.
- Grant M.C., C. Orsman, J. Easton, C. Lodge, M. Smith, G. Thompson, S. Rodwell & N. Moore 1999. Breeding success and causes of breeding failure of Curlew *Numenius arquata* in Northern Ireland. Journal of Applied Ecology 36: 59-74.
- Grant M.C. 2002. Effects of radiotagging on the weight gain and survival of Curlew *Numenius arquata* chicks. Bird Study 49: 172-176.
- Green R.E. 1988. Effects of environmental factors on the timing and success of breeding of Common Snipe *Gallinago gallinago* (Aves, Scolopacidae). Journal of Applied Ecology 25: 79-93.
- Green R.E., G.J.M. Hirons & J.S. Kirby 1990. The effectiveness of nest defence by Black-tailed Godwits *Limosa limosa*. Ardea 78: 405-413.
- Green R.E. 2002. Diagnosing causes of population declines and selecting remedial actions. In: Norris K. & D.J. Pain (eds.). Conserving Bird Biodiversity: 139-156. Cambridge University Press, Cambridge.
- Kaplan E.L. & P. Meier 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53: 457-481.

- Kenward R.E., P.A. Robertson, A.S. Coates, V. Marcström & M. Karlbom 1993. Techniques for radiotagging Pheasant chicks. Bird Study 40.
- Korschgen C.E., K.P. Kenow, W.L. Green, D.H. Johnson, M.D. Samuel & L. Sileo 1996. Survival of radiomarked Canvasback ducklings in northwestern Minnesota. Journal of Wildlife Management 60: 120-132.
- Krapu G.L., P.J. Pietz, D.A. Brandt & R.R. Cox 2006. Mallard brood movements, wetland use, and duckling survival during and following a prairie drought. Journal of Wildlife Management 70: 1436-1444.
- Langgemach T. & J. Bellebaum 2005. Predation and the conservation of ground-breeding birds in Germany. Die Vogelwelt 126: 259-298.
- Larson M.A., M.E. Clark & S.R. Winterstein 2001. Survival of Ruffed Grouse chicks in northern Michigan. Journal of Wildlife Management 65: 880-886.
- Miller B.J. & F.L. Knopf 1993. Growth and survival of Mountain Plovers. Journal of Field Ornithology 64: 500-506.
- Ottvall R. 2005. Breeding success and adult survival of Redshank *Tringa totanus* on coastal meadows in SE Sweden. Ardea 93: 225-236.
- Payne R. 2005. The guide to Genstat release 8. Part 2: Statistics. VSN International, London.
- Peach W.J., P.S. Thompson & J.C. Coulson 1994. Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. Journal of Animal Ecology 63: 60-70.
- Pearce-Higgins J.W. & D.W. Yalden 2003. Golden Plover *Pluvialis apricaria* breeding success on a moor managed for shooting Red Grouse *Lagopus lagopus*. Bird Study 50: 170-177.
- Pietz P.J., G.L. Krapu, D.A. Brandt & R.R. Cox 2003. Factors affecting gadwall brood and duckling survival in Prairie Pothole Landscapes. Journal of Wildlife Management 67: 564-575.
- Ratcliffe N., Schmitt S. & Whiffin M. 2005. Sink or swim? Viability of a Black-tailed Godwit population in relation to flooding. Journal of Applied Ecology 42: 834-843.
- Riley T.Z., W.R. Clark, D.E. Ewing & P.A. Vohs 1998. Survival of ring-necked pheasant chicks during brood rearing. Journal of Wildlife Management 62: 36-44.
- Schekkerman H. & G. Müskens 2000. Produceren Grutto's *Limosa limosa* in agrarisch grasland voldoende jongen voor een duurzame populatie? Limosa 73: 121-134.
- Schekkerman H. & G.H. Visser 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. Auk 118: 944-957.
- Schekkerman H., W. Teunissen & E. Oosterveld 2005. Broedsucces van grutto's bij agrarisch mozaïekbeheer in 'Nederland Gruttoland'. Alterra-rapport 1291, Alterra, Wageningen.
- Schekkerman H. & A.J. Beintema 2007. Abundance of invertebrates and foraging success of Black-tailed Godwit (*Limosa limosa*) chicks in relation to agricultural grassland management. Ardea 95: 39-54.
- SOVON 2002. Atlas van de Nederlandse broedvogels 1998-2000. Nationaal Natuurhistorisch Museum Naturalis, Leiden.
- Swennen C. 1989. Gull predation upon Eider *Somateria mollissima* ducklings - destruction or elimination of the unfit? Ardea 77: 21-45.
- Teunissen W. 2007. Afname van weidevogels versnelt sinds eeuwwisseling. SOVON-nieuws 20: 15-17.
- Teunissen W.A., Schekkerman H. & Willems F. 2005. Predatie bij weidevogels. SOVON-onderzoeksrapport 2005/11. SOVON, Beek-Ubbergen.

- Teunissen W., Schekkerman H. & Willems F. 2006. Predation on meadowbirds in The Netherlands: results of a four-year study. Osnabrücker Naturwissenschaftliche Mitteilungen 32: 137-143.
- Teunissen W.A. & L.L. Soldaat 2006. Recente aantalsontwikkeling van weidevogels in Nederland. De Levende Natuur 107: 70-74.
- Teunissen W., H. Schekkerman, F. Willems & F. Majoor submitted. Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. Submitted manuscript.
- Thorup O. 2006. Breeding waders in Europe 2000. International Wader Studies 14. International Wader Study Group, UK.
- Vickery J.A., J.R. Tallowin, R.E. Feber, E.J. Asteraki, P.W. Atkinson, R.J. Fuller & V.K. Brown 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38: 647-664.
- Whittingham M.J., S.M. Percival & A.F. Brown 1999. Evaluation of radiotelemetry methods in measuring habitat choice by young Golden Plover *Pluvialis apricaria* chicks. Bird Study 46: 363-368.
- Wilson A.M., M. Ausden & T.P. Milsom 2004. Changes in breeding wader populations on lowland wet grasslands in England and Wales: causes and potential solutions. Ibis 146 (Suppl. 2): 32-40.

9

Synthesis

ECOLOGICAL CONSEQUENCES OF SELF-FEEDING PRECOCIALITY

The altricial-precocial spectrum is an axis of gradual transitions, involving variation in multiple characters and with many species occupying intermediate positions between the fully altricial and fully precocial modes of development. Nevertheless, some transitions within this spectrum may have more profound ecological and evolutionary consequences than others. Ricklefs & Starck (1998b) stressed two primary distinctions within the spectrum: that between truly altricial species (uniquely characterized by a low level of functional maturity at hatching) and all other birds, and that between nidicolous (nest-staying) and nidifugous (nest-fleeing) species, with consequences for both morphology (maturity of neuromotor control systems) and behavioural ecology (predator avoidance, food provisioning economy). In this thesis I have highlighted the importance of a third distinction, that between parent-fed and self-feeding chicks. Although this transition does not seem to be associated with abrupt changes in morphology or level of functional maturity of specific organ systems at hatching (Starck & Ricklefs 1998), the shift of food acquisition from parents to chicks is bound to represent a major change in the feeding ecology of the family unit. While it is expected to reduce energetic stress for parent birds, for the chicks the need to forage for themselves is likely to lead to increased energy requirements and vulnerability to fluctuations in food availability.

Chick energy requirements

Weathers (1992, 1996) reviewed available estimates of the total amount of energy metabolised over the prefledging period (TME) in 30 bird species (28 of which feed their young), and showed that TME is strongly influenced by body mass and age at fledging. The first is straightforward, the second arises because the costs of basal metabolism, thermoregulation and activity accumulate over a longer period in slow-growing species. In chapters 2 and 3 we measured the energetic consequences of a self-feeding precocial lifestyle for shorebird chicks in the field. In comparison with Weathers' allometric prediction, TME was 29-39% higher in the temperate Black-tailed Godwit and Northern Lapwing, and 89% higher in the arctic Red Knot. Moreover, the allocation of the energy budget of shorebird chicks also differed from that in seven parent-fed bird species, with a much higher proportion of the total metabolised energy allocated to thermoregulation and activity, and less to growth production. This difference was upheld in a comparison with a larger sample of 12 parent-fed species, including some with high thermoregulatory demands (Weathers *et al.* 2003).

Since the publications of Weathers (1992, 1996), additional studies of prefledging energy requirements in birds have been published. Several of these also concerned shorebirds and although some also reported very high TME (Tjørve *et al.* 2007a), others seemed to differ less from the allometric prediction (Joest 2003, Tjørve *et al.* 2007b, 2007c, Tjørve *et al.* 2008). Other studies reported high energy requirements also in parent-fed birds, mostly seabirds breeding in arctic and antarctic environments (Gabrielsen *et al.* 1992, Konarzewski *et al.* 1993, Obst & Nagy 1993, Klaassen 1994, Hodum & Weathers 2003). In addition to fledgling size and age, the thermal environment (climate) is also expected to affect TME, through thermoregulation costs but possibly also through

TABLE 9.1. Estimates of avian prefledging energy requirements obtained with the doubly labeled water method in the field. Given are developmental type (M: 1 parent-fed in nest, 2 fed outside nest, 3 self-feeding), latitude of study area (Lat), ambient temperature (T_a, with note on source if not reported in the primary paper), fledgling mass (M_{fl}), duration of prefledging period (T_{fl}), Total Metabolised Energy (TME), Peak Metabolised Energy (PME) and data source.

Nr	Species	M	Lat °	T_a °C	Mfl g	Tfl days	TME kJ	PME kJ/d	Source
1	Savannah Sparrow *Passerculus sandwichensis*	1	34	16	13	8	247	48.6	1
2	Yellow-eyed Junco *Junco phaeonotus*	1	35	17	17	9	322	59.5	2
3	White-crowned Sparrow *Zonotrichia leucophrys*	1	39	13	21	9	443	71.2	3
4	Dune Lark *Mirafra erythroclamys*	1	24	21	23	14	464	65.2	4
5	Western Bluebird Sialia mexicana	1	33	13	28	21	1110	65.4	5
6	Ashy-throated Flycatcher *Myiarchus cinerascens*	1	33	18	28	17	1024	71.8	5
7	Arabian Babbler *Turdoides squamiceps*	1	30	23	46	14	759	122	6
8	Southern Grey Shrike *Lanius meridionalis*	1	31	18	50	18	1146	119	7
9	Acorn Woodpecker *Melanerpes formicivorus*	1	37	14	81	31	3853	146	8
10	Eurasian Sparrowhawk *Accipiter nisus*	1	53	13	167	24	4525	313	9 *
11	Snow Petrel *Pagodroma nivea*	1	69	0[a]	246	47	17637	334	10
12	Eurasian Sparrowhawk *Accipiter nisus*	1	53	13	270	24	6435	484	9 *
13	Kittiwake *Rissa tridactyla*	1	79	5	399	35	18400	588	11
14	Cape Petrel *Daption capense*	1	69	0[a]	441	47	31728	567	10
15	Antarctic Petrel *Thalassoica antarctica*	1	69	0[a]	590	48	31657	732	10
16	Southern Fulmar Fulmarus glacialoides	1	69	0[a]	808	52	50692	941	10
17	Arctic Tern *Sterna paradisaea*	2	53	13[b]	107	22	3996	217	12
18	Common Tern *Sterna hirundo*	2	53	13[b]	114	25	4852	218	12
19	Arctic Tern Sterna paradisaea	2	79	5[c]	115	22	4628	234	12
20	Antarctic Tern *Sterna vittata*	2	62	4[c]	133	27	7150	244	12
21	Black-headed Gull *Larus ridibundus*	2	53	13[b]	225	30	9190	373	13 *
22	Spotted Thick-knee *Burhinus capensis*	2	34	19	386	54	17546	474	14 *
23	Afr. Black Oystercatcher *Haematopus moquini*	2	34	21	463	40	17267	635	15 *
24	Adélie Penguin *Pygoscelis adeliae*	2	65	3[d]	3200	50	111780	3342	16
25	Little Stint C*alidris minuta*	3	74	8	22	15	1348	61.5	17 *
26	Kittlitz' Plover Charadrius pecuarius	3	34	20	28	30	1379	56.2	18 *
27	Blacksmith Lapwing *Vanellus armatus*	3	34	14	106	40	4506	166	18 *
28	Red Knot *Calidris canutus*	3	75	1	108	18	5285	238	19 *
29	American Golden Plover *Pluvialis dominica*	3	59	17	111	22	5019	224	20 *
30	Crowned Lapwing *Vanellus coronatus*	3	34	20	117	35	4527	193	18 *
31	Northern Lapwing *Vanellus vanellus*	3	52	14	142	33	6982	236	21 *
32	Pied Avocet *Recurvirostra avosetta*	3	36	23	175	35	7951	278	22 *
33	Pied Avocet *Recurvirostra avosetta*	3	54	13	192	35	8423	302	22 *
34	Black-tailed Godwit Limosa limosa	3	52	14	201	25	8331	364	21 *

[a] From Hodum 2002; [b] KNMI weather data; [c] based on nr 13 and measured T_e; [d] Palmer Station climate data

Sources: 1 Williams & Prints 1986, 2 Weathers & Sullivan 1991, 3 Weathers *et al*. 2003, 4 Williams 2001, 5 Mock *et al*. 1991, 6 Anava *et al*. 2001, 7 Degen *et al*. 1992, 8 Weathers *et al*. 1990, 9 Vedder *et al*. 2005, 10 Hodum & Weathers 2003, 11 Gabrielsen *et al*. 1992, 12 Klaassen 1994, 13 Eising in Tjørve 2006, 14 Tjørve *et al*. 2007b, 15 Tjørve *et al*. 2007c, 16 Janes 1997, 17 Tjørve *et al*. 2007a, 18 Tjørve *et al*. 2008, 19 Schekkerman *et al*. 2003, Chapter 3, 20 Visser *et al* in Tjørve 2006, 21 Schekkerman & Visser 2001, Chapter 2, 22 Joest 2003.

Studies marked with an asterisk * were initiated or supported by the late Henk G. Visser.

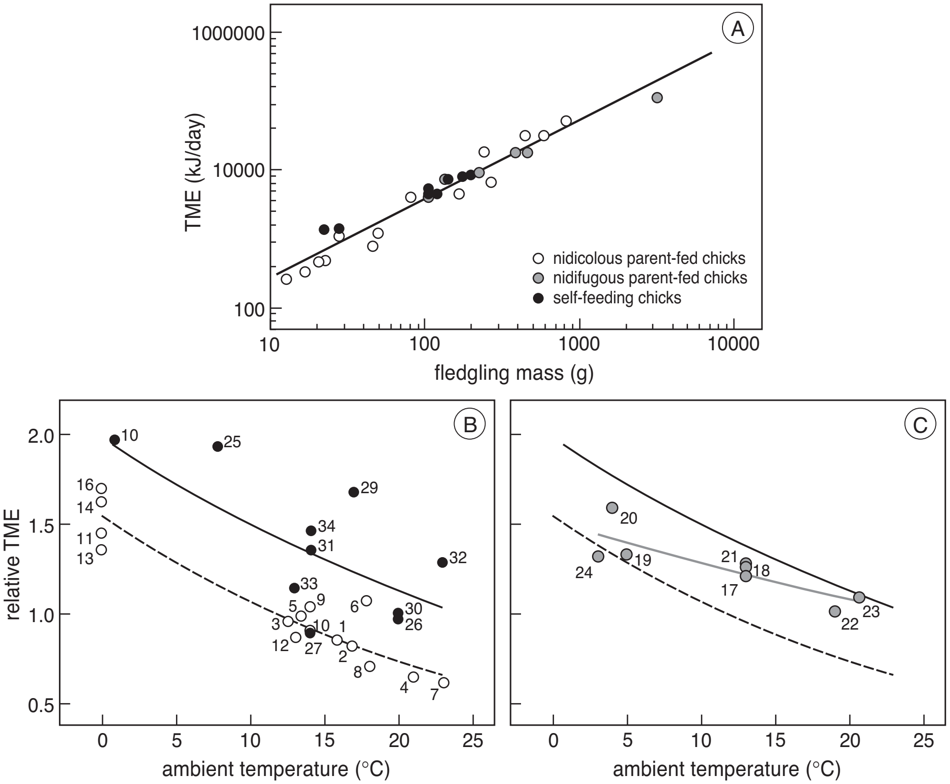
changes in basal metabolism reflecting the size and activity of organs involved in thermoregulation and growth (Weathers 1992, Klaassen & Drent 1991). In comparing energy requirements between species or developmental modes, it is thus important to include climate as a covariate. The method employed to measure chick metabolism is another potential confounding factor, as estimates based on food calorimetry and respirometry are generally less accurate than doubly labelled water measurements (Weathers 1992), and can underestimate TME as thermoregulation and activity costs may be substantially less in a laboratory setting than under field conditions (Chapter 2, Williams & Prints 1986, Klaassen 1994 *vs.* Drent *et al.* 1992).

Therefore I have collated all 34 published estimates (in 32 bird species) of chick energy requirements known to me that were obtained in the field using the doubly labeled water (DLW) method (table 9.1), and explored the dependence of TME and Peak Metabolised Energy (PME, the highest ME at any age during the prefledging period) on fledgling mass (M_{fl}), fledgling age (T_{fl}), ambient temperature (T_a) and developmental mode. I used T_a as a climate variable rather than latitude, because data from the same latitude may hide substantial (e.g. altitudinal or seasonal) temperature variation. I classified species into developmental groups based on feeding mode and mobility: (1) parent-fed chicks that stay in a nest or burrow throughout the prefledging period (altricial, semialtricial or semiprecocial), (2) parent-fed semiprecocial chicks that wander outside the nest (even if only for short distances within a breeding colony) and (3) self-feeding precocials. The data were analysed using linear regression, treating all estimates as statistically independent, although a pylogeny-based analysis would be preferable. TME, M_{fl} and T_{fl} were log-transformed to homogenise variances and allow for non-linear relationships.

Both fledging mass and time to fledging have a strong positive effect on TME in the DLW-based dataset (fig. 9.1, table 9.2). The scaling exponents are similar to those reported by Weathers (1992) from his partly overlapping sample (M_{fl} 0.78 *vs.* Weathers 0.85, T_{fl} 0.66 *vs.* 0.71). A decrease of TME with increasing ambient temperature is apparent in all developmental groups (fig. 9.1b, table 9.2). With these effects controlled for, developmental type also significantly affects chick energetics: TME of self-feeding chicks is higher than that of nidicolous parent-fed young over the entire temperature range, by *c.* 40% on average. It is noteworthy that the difference between these groups does not become larger at low temperature despite the fact that the former are more exposed to its cooling effect. Interestingly, the two precocial species that deviate most from the temperature relationship were both measured at the edge of their breeding distributions. Blacksmith Lapwings (nr. 27 in fig 9.1) have only recently expanded their former breeding range in the summer rainfall area of southern Africa to include the (winter rainfall) Western Cape region without shifting their breeding phenology, so that their chicks grow up here under atypically cold and wet conditions (Tjørve *et al.* 2008). Conversely, American Golden Plovers (nr. 29) breed nowhere further south than the study site at Churchill, Canada. The fact that the former metabolise less and the latter more energy than predicted from the local temperature regime suggests that chick metabolism not only reflects actual demands for thermoregulation but also a 'ghost' of physiological adaptations to the species' general breeding climate (expressed in e.g. resting metabolism and growth rate).

TME of nidifugous parent-fed chicks seems to bridge the difference between that of nidicolous and self-feeding species, and overlaps with the former at the low and with the latter at the high end of the temperature range (fig. 9.1c). One would expect TME to correlate with the level of mobility outside the nest, and this may explain the nearly significantly shallower slope of the temperature effect in this group. The two 'warm' datapoints are for Spotted Thick-knee and African Black Oystercatcher chicks that follow their parents on the feeding grounds (older thick-knees even feed for themselves to some extent).

FIGURE 9.1. Total Metabolised Energy of growing birds in the field obtained with the doubly labelled water method, in relation to fledgling mass (A), ambient temperature and developmental type (B-C). In (B), relative TME (observed TME divided by the value predicted at the species' fledging mass and age at the average ambient temperature for the whole sample) is shown for self-feeding chicks and chicks fed by parents while staying in a nest; B shows TME for parent-fed chicks that wander outside a nest. Data labels refer to species numbers in table 9.1. The regression line in A is for the entire sample of 34 estimates, those in B and C are based on the regression model in table 9.2. Regression lines from B are repeated in C to aid comparison.



The highest energy requirement at any age during the prefledging period (PME) shows a pattern with developmental mode similar to TME, being highest in self-feeding precocials, intermediate in nidifugous parent-fed species and lowest in nidicolous birds (table 9.2). Although there was a weak tendency for PME to decrease with growth rate (as less energy is deposited into new tissue per day), this effect was not significant.

The DLW-based data accumulated in recent years thus support the idea that precocial chicks are energetically expensive due to high costs of thermoregulation and (foraging) activity. However, there is a clear need for measurements in additional species. The presently available TME estimates for self-feeding precocials are from shorebirds only, and should be augmented with field measurements in groups like geese, ducks and galliforms in various climates. Only a few estimates are available for parent-fed chicks that follow their parents over longer distances (two shorebirds, but no cranes, rails, bustards, divers and grebes, etc.), which makes it difficult to distinguish the effects of being 'merely' nidifugous from that of self-feeding. Within nidicolous parent-fed species there is need for wider sampling according to hatchling functional maturity, phylogeny and climate: the available 'warm' data are mostly from altricial passerines (often from deserts; none from tropical forests), while those from cold climates are from semialtricial and semiprecocial seabirds (Procellariiformes and Charadriiformes), and many other nidicolous orders are not represented at all.

TABLE 9.2. Regression analysis (forward addition of terms) of Total Metabolised Energy (TME) and Peak Metabolised Energy (PME) for species shown in table 9.1 and fig. 9.1.

Variables	d.f.	S.S.	F	P	term	estimate	S.E.
log TME (kJ)							
Total	33	71.495			constant	2.978	0.314
+ Fledging mass	1	67.701	3259.8	<.001	log(M_{fl})	0.7777	0.0443
+ Fledging time	1	0.397	79.71	<.001	log(T_{fl})	0.662	0.119
+ Ambient temperature	1	1.065	51.29	<.001	T_a	−0.04533	0.00695
+ Developmental type	2	0.397	9.55	<.001	type 2	−0.125	0.134
					type 3	0.075	0.155
+ Ta x Development type	2	0.137	3.30	0.053	T_a x type 2	0.0291	0.0113
Residual	26	0.540			T_a x type 3	0.0180	0.0118
log PME (kJ/d)							
Total	32	28.556			constant	2.403	0.223
+ Fledging mass	1	25.664	674.01	<.001	log(M_{fl})	0.7129	0.0392
+ Fledging time	1	0.124	3.26	0.083			
+ Ambient temperature	1	0.682	17.91	<.001	T_a	−0.02976	0.00608
+ Developmental type	2	1.122	14.73	<.001	type 2	0.1140	0.1010
					type 3	0.3865	0.0877
+ Ta x Development type	2	0.012	0.16	0.855			
Residual	25	0.952					

TABLE 9.3. Possible selective factors affecting developmental mode in birds. From bottom to top, three major dichotomies in the gradient from altricial to fully precocial development are indicated, and hypothetical effects on the ecological and evolutionary success of birds exhibiting these characteristics are outlined. Consequences of hatchling functional maturity according to Ricklefs & Starck (1998b).

Increasing precociality

State	Mechanism	Ecological / evolutionary consequence
Self-feeding (vs. parental feeding)	• Loss of a parent (or both) less likely to preclude chick survival	• Reduced vulnerability to adult mortality/desertion, favours polygamy
	• Parents do not spend time and energy on feeding chicks	• Smaller investment per offspring allows larger brood or higher future reproduction
	• Four (or six, or ten) chicks may gather more food than two adults	• Allows larger brood size (if limited by adult foraging potential) or exploiting less nutritive food
	• Foraging performance may depend on chicks' own nutritive condition (negative condition spiral)	• Increased vulnerability to short-term variation in food availability
	• Foraging outside the nest increases chick energy expenditure and food demand	• Dependence on high food availability
	• Profitability of food items not reduced by time spent transporting to young	• Items with lower energy yield (small, vegetable) can be exploited as chick food
	• Chicks cannot procure food items requiring strength or intricate cognitive/motor capabilities, including flight and diving	• Limits offspring food types and foraging habitats (to ground or water surface)
	• No repeated parental food deliveries to chicks that facilitate detection by predators	• Reduced vulnerability to chick predation
	• High energy expenditure and/or growth-maturity trade-off decrease rate and efficiency of growth	• Longer fledging period prolongs exposure to chick predators
Nidifugy (vs. nest attendance)	• Chicks can be led to food: lower transport cost reduces parental energy expenditure	• Smaller investment per offspring allows larger brood or higher future reproduction
	• Chicks can be led to food: lower transport time allows higher food delivery rate	• Items with lower energy yield can be exploited as chick food
	• Activity of chicks outside nest facilitates detection by predators	• Increased vulnerability to chick predation
	• Mobile broods may avoid danger from predators	• Reduced vulnerability to chick predation
	• Predators less likely to find all chicks at once	• Reduced vulnerability to chick predation
Hatchling maturity (high vs low)	• Trade-off between growth and maturation at tissue level reduces postnatal growth rate	• Prolongs fledging period, increases vulnerability to chick predation
	• Trade-off between growth and maturation at tissue level reduces brain growth and adult brain size	• Altricial development allows large adult brains suitable for active lifestyle and small adult size
	• Lower metabolism of less matured embryo in late egg stage avoids limitation by oxygen supply that would reduce growth rate	• Very short incubation periods, reducing exposure to egg predators, only possible in altricials

Sensitivity to short-term food shortage

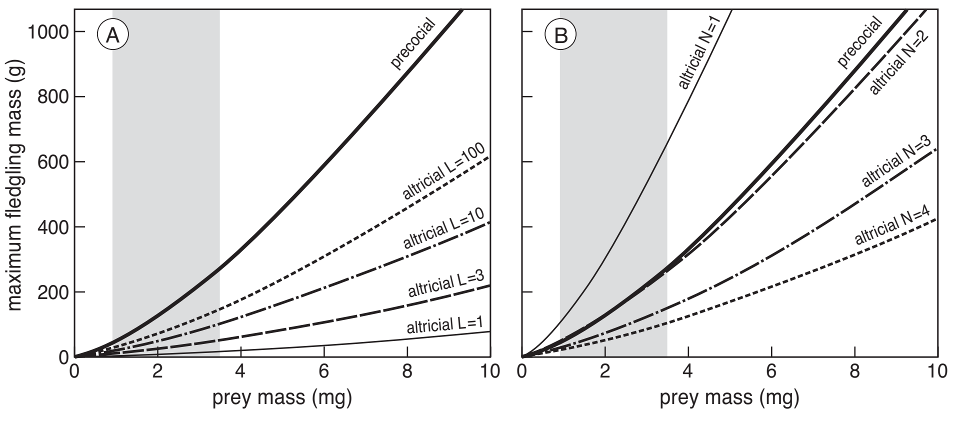
In addition to requiring more food than parent-fed young, self-feeding chicks may be more sensitive to short-term food shortage. Parent-fed nestlings may simply sit out a few days of severe weather that impairs their parents' foraging success, and may even save energy by reducing activity (Klaassen *et al.* 1994). If conditions are not too bad, one parent may go on collecting food while the other broods the chicks. As soon as the weather improves, parents can return food delivery to normal levels or even beyond to allow chicks to catch up in lost growth. For self-feeding chicks, increase of brooding and reduction of feeding activity during adverse weather reduces food intake and is likely to compromise growth even further, especially as the fraction of total energy turnover that is allocated to growth is smaller in such species (Chapter 2). In addition, it may be harder for a self-feeding chick to catch up when conditions improve, either because it was already feeding at maximum capacity under 'normal' conditions, or because lagging behind in growth reduces its performance. In chapter 5 we investigated whether a poor body condition affected the foraging of godwit chicks. We found that chicks in poor condition were brooded for a larger proportion of the time than same-age chicks of normal weight, leading to a reduction in time available for foraging. This effect is largest under cold and wet conditions when brooding time is substantial, and diminishes as weather improves. We did not observe a significant negative effect of chick condition on foraging success. Energy expenditure will also be reduced in chicks in poor condition, and this may compensate at least in part for shortfall in energy acquisition, so that it is hard to say whether the net effect is a genuine risk for chicks to end up in a negative condition spiral. However, we did observe that radio-tagged godwit chicks in poor condition are more likely to die than same-age chicks growing normally, not only from starvation but also from other causes, probably including predation (Chapter 8).

Chick diets

Self-feeding precocial birds thus require both abundant and dependable food sources for successful growth (table 9.3). In addition, the self-feeding mode impinges on the quality of chick diets. In their discussion of the evolution of avian developmental modes Ricklefs & Starck (1998b) asserted that "the quality of the diet can be eliminated immediately as a selective factor because one finds more or less the full range of food types among each of the modes of development". However, self-feeding precludes certain food types and even entire habitats to be exploited as a chick food resource, and many of the food types that require cognitive or motor skills beyond the abilities of young birds but not of feeding parents are of high quality because of their size or nutrient composition. Fish, reptiles, mammals, birds, crustaceans, clams and snails, and certain buried invertebrates are examples of such food types; there are few self-feeding precocials that regularly include these in their diet as a chick.

On the other hand, the self-feeding mode is well suited to exploit food items of small size or low nutritive quality. First, provided that there are more chicks than adults, self-feeding can increase the total encounter rate of food items by the brood unit, as there are simply more foragers. Second, the items encountered do not require transportation to a central place. Whereas the energy cost of food transport is paid by the parents, the time cost is felt by parent-fed chicks as well, as it reduces the rate at which adults can deliver prey. This profitability loss is largest for small or low-energy food items. For these reasons, chick-feeding parent birds will be limited in their ability to supply their brood's needs at a larger average size or higher nutritive quality of prey than chicks that feed for themselves. Figure 9.2 illustrates this point with a simple model based on the criterion that reproduction can be successful only if either the (precocial) chicks themselves or two (altricial) parents can satisfy the brood's peak energy requirements in a single foraging day. Adaptations enabling multiple-prey loading by parents reduce the cost of prey transport, but usually only partly, and they are not present in all chick-feeding birds.

FIGURE 9.2. How the average size of prey can limit the size distribution of birds depending on developmental mode, brood size and potential for multiple-prey loading. The principle is shown here for a situation similar to that encountered by insectivorous birds in a Dutch meadow, based on a simple model assuming that reproduction is successful only if either the (precocial) chicks themselves or two (altricial) parents can satisfy the brood's peak energy requirements in a 14-hour foraging day. PME (kJ/d/chick) was calculated as in table 9.2 for T_a=15°C. Other assumptions were that prey contain 23 kJ energy per g dry mass of which 74% is assimilated, are encountered at a rate of 1 per 5 seconds and require 1 s to manipulate (*cf*. Black-tailed Godwit chicks, Chapter 5), and that each food delivery by a parent takes 2 x 10 s flying (*c*. 80 m at 30 km/h) plus 2 s for prey handover. The model does not include energy costs of prey transport for parents. A: maximum fledgling mass as a function of prey mass for self-feeding precocials (thick line, independent of brood size) and for altricial broods containing 4 nestlings, depending on the number of prey items L that can be loaded on a single flight. B: maximum fledging mass as a function of brood size N for altricials loading 10 prey items per flight. The grey columns show average prey sizes taken by godwit chicks in grasslands managed as a meadowbird reserve.



Food types like small invertebrates, herbage and other plant material form the staple diet of chicks of many self-feeding precocial birds, even among those with an intermediate or large body size like galliforms, ostriches, geese and swans. Generally, exploitation of such food to feed offspring is more strongly limited to small species (up to starling size) in parent-fed and nidicolous groups. There is only one nidicolous bird with truly herbivorous chicks: the Hoatzin *Opisthocomus hoazin,* and these are fed with leaf mash already partially digested by their parents. Hence, the abundance and quality of various types of food have been important factors in shaping the evolutionary success of developmental modes under different ecological conditions.

Other consequences

The absence of a need to collect and transport food for young is likely to reduce the energetic costs of raising young to its parents. While the field metabolic rate (FMR) of parent birds caring for young has been measured in several tens of bird species (reviews by Bryant & Tatner 1991, Tinbergen & Williams 2002), to my knowledge only three have concerned birds with self-feeding chicks. Tatner & Bryant (1993) measured FMR of both incubating and chick-rearing Common Sandpipers *Actitis hypoleucos*, while Tulp *et al.* (2007) did so in Dunlin *Calidris alpina* and Little Stint *C. minuta*. The data are still too scant for a rigorous comparison, but as yet they provide no evidence for a reduction of parental energy expenditure during the chick phase (Tulp *et al.* 2007). Clearly, there is a need for more measurements in precocial parents; if these are combined with measurements on chicks this will also allow comparing energy budgets at the level of the family unit. However, Bryant & Tatner (1991) did find that parental energy expenditure increases with brood provisioning rate and proportion of time spent flying within parent-fed species, and this suggests that absence of feeding flights will indeed reduce parental DEE. This will be partly offset by an increase in energy requirements for egg production and incubation, as precocial birds tend to lay larger eggs that must be incubated longer (Ricklefs & Starck 1998a). Nevertheless, the period of provisioning food to nestlings or recently-fledged young is an energetically demanding phase in the annual cycle of many birds (Weathers & Sullivan 1993), and a reduction of energy investment per chick may allow avian parents to provision a larger brood or multiple broods within a year, or achieve higher future reproductive success via a prolonged breeding lifespan due to improved adult survival (table 9.3).

The consequence of desertion (or death) of one or both parents for the survival of chicks to independence is likely to be less severe in self-feeding than in parent-fed birds (though there may be exceptions, like geese), and this may ‘free’ the parents to pursue alternative reproductive strategies including polygamy. In a comparative analysis among bird species, Temrin & Tullberg (1995) found that the pair bond more often dissolves before hatching of the young in nidifugous than in nidicolous birds, and that (females of) species with nidifugous chicks are more often polygamous. Thomas & Szekely (2005) showed that within the order Charadriiformes, evolutionary change from parental feeding to self-feeding preceded change from care for the young by both parents to uniparental care (by either males or females), associated with change to mating systems other than monogamy. The latter in turn promotes the diversification of secondary sexual characters, most notably sexual size dimorphism (Thomas *et al.* 2006).

Developmental mode may also impinge on predation risk, though nidifugy and self-feeding may have both positive and negative consequences in this respect (table 9.3). Predation may be avoided when broods leave the nest and can move away from the vicinity of predators, when chicks hide in separate places so that they cannot be found simultaneously, and when parents do not make repeated feeding visits to a central place. On the other hand, chicks that forage actively may become more conspicuous to predators, and precociality is associated with longer incubation and fledging periods which prolong exposure to predation. It is also easier to select safe nest sites like trees and cavities when food is delivered to the young, though examples of tree-nesting (e.g. Green Sandpiper *Tringa ochropus*, Egyptian Goose *Alopochen aegyptiacus*) and cavity-nesting precocials (many ducks) are fairly numerous. The net result is therefore not so easily predicted, and may differ according to bird species, predator species and habitat. All in all, there seems to be extensive overlap in overall daily mortality rates between chicks of different developmental modes (Ricklefs *et al.* 1998).

ARCTIC TUNDRA: A HOT SPOT FOR PRECOCIAL CHICKS

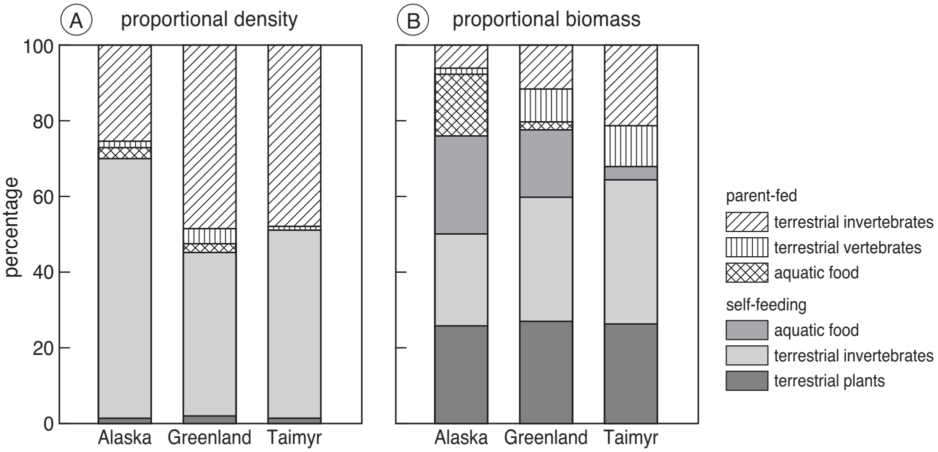
The analysis presented in figure 9.1 and table 9.2 confirmed the strong influence of climate on chick energy requirements. In arctic-breeding birds, the activity cost associated with self-feeding precocial development is added onto the high thermoregulation demands imposed by the arctic climate, resulting in very high TME (fig. 9.1). In addition, the potential to satisfy these high energy requirements will be reduced by an increased need for parental brooding in the cold climate (Chappell 1980), as young shorebirds chicks are rather thermolabile in comparison to other precocials like Anseriformes and Galliformes. In chapter 3 we showed that an increased cold-hardiness and a fast growth rate are adaptations that help arctic-breeding shorebirds overcome this foraging time limitation (see also Krijgsveld *et al.* 2001). However, these same adaptations are likely to further increase the chicks' daily energy requirements, because they entail higher activity of organs involved in heat generation, food processing and tissue formation. The growth strategy of shorebirds (and arctic birds in general, see Carey 1986, Klaassen & Drent 1991, Fortin *et al.* 2000) for coping with the difficulties of the arctic climate thus seems to be one of "attack is the best defense". Nevertheless, it is not all sunshine in the Arctic, and variation in weather and surface-activity of invertebrates have pronounced effects on chick growth rate (Chapter 3, Tulp & Schekkerman 2007). The analysis in chapter 4 showed that in the Curlew Sandpiper *Calidris ferruginea*, annual variation in weather conditions on the Siberian tundra during the early chick phase is parallelled by variation in the proportion of juveniles in the 'wintering' population in South Africa, which is evidence for a strong survival effect. Similar observations have subsequently been reported by Morrison (2004) and Beale *et al.* (2006).

Shorebirds with an arctic breeding distribution are much more common among families with self-feeding young than among groups with parental feeding, and the arctic tundra biome is a 'hot spot' of precocial shorebird biodiversity, especially in the Scolopacidae (table 1.1). Throughout the circumpolar tundra biome, shorebirds make up a large proportion of the terrestrial bird community (fig. 9.3). Apparently, the arctic tundra does have something to offer that suits the high-cost ontogeny of self-feeding shorebirds, but what is it?

The uninterrupted period of daylight during the arctic summer allows foraging time for diurnal animals to be prolonged compared to lower latitudes, increasing the amount of energy that can be assimilated per day (Kvist & Lindström 2000). However, the high-arctic Red Knot chicks studied in chapter 3 did not fully utilize the continuous daylight, and were brooded more during the period of lowest light levels than expected from the low temperatures also occurring at this time of 'day'. Tjørve *et al.* (2007a) observed the same in Little Stint chicks at 73°N. Whether this pause at night occurred because chicks chose to give up foraging sooner at 'night' because intake rate no longer matched energy expenditure as arthropod activity was reduced by low temperature and/or light levels, or because of a need for sleep in the chicks is an unresolved question. Our poor understanding of patterns of sleep in birds (Roth *et al.* 2006) thus precludes a full evaluation of the role of daylight as a factor limiting bird distributions.

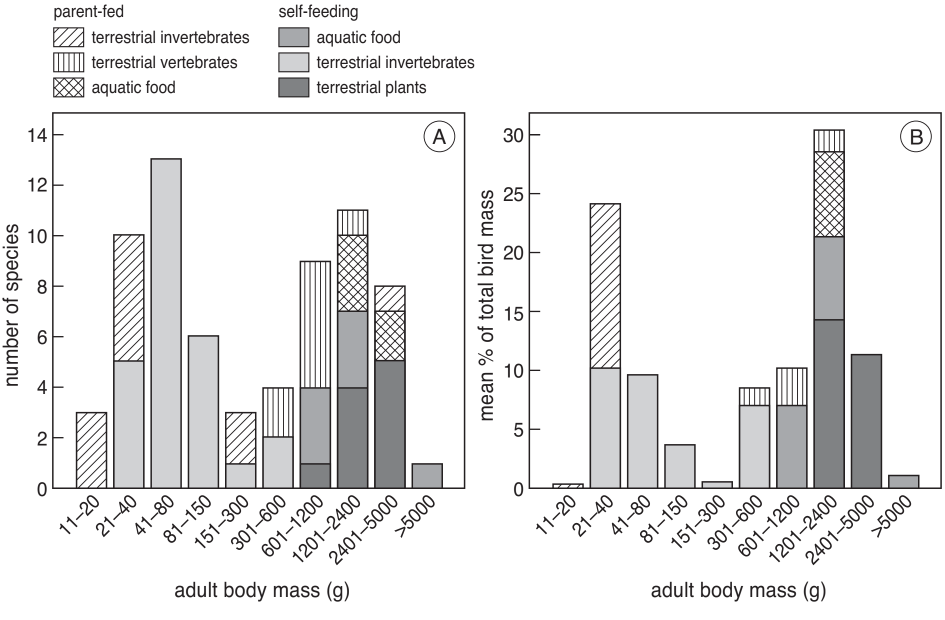
A second potential factor enabling shorebirds to breed in the arctic is a high availability of food. Primary and secondary production within ecosystems generally decreases with latitude, but in arctic tundras this production is concentrated in a short burst, exemplified by the midsummer emergence peak of midges and other arthropods (Maclean & Pitelka 1971, Danks 1999, Tulp & Schekkerman 2008). Several authors have stressed the high abundance of food for insectivorous birds during this peak period, also in comparison to temperate latitudes (Lack 1968, Salomonsen 1972, Andreev

FIGURE 9.3. Chick diets of the terrestrial bird fauna of three high-arctic tundra sites: Prudhoe Bay, N-Alaska, 70°N (Troy 1996), 14 sites in NE-Greenland, 76-78°N (Boertmann *et al.* 1991) and Medusa Bay, NW-Taimyr, 74°N (Willems *et al.* 2002). Breeding densities (A; nests or pairs /km²) and biomass (B; kg/km²) were summed over categories of feeding mode and chick food type. Species exploiting marine food resources (larger gulls, Arctic Tern, auks) are not represented. Biomass was calculated as the sum over species of (breeding density x adult body mass x (number of parents attending each brood + 0.7 x mean brood size).



1999), but few studies have quantitatively compared biomass or densities of arthropods between arctic and temperate shorebirds habitats. Our sampling revealed lower rather than higher abundance of surface-active arthropods in a site in northern Siberia than in a temperate grassland (Chapter 3). It is not clear how general this finding is, but the mean number of arthropods caught per pitfall per day during the chick period at Cape Sterlegov in 1991 (*c.* 7, excluding mites and springtails) was similar to that in a different site on Taimyr in 2000-2003 (4-9, Tulp & Schekkerman 2008). In NE Greenland slightly higher abundances were recorded in lowland tundra in 1996-2003 (7-13; Rasch & Caning 2004), but in 2007 we recorded only 2-3 animals/trap/day here at elevations >100 m a.s.l. (I. Tulp, J. Reneerkens, J. Jukema, K. Dijksterhuis & HS unpubl. data). The critical feature however is not density or biomass *per se* but the harvestability of prey items to the birds. The simulation model that we constructed on the basis of our observations in chapter 3 implied that Red Knot chicks can grow as fast as they do in the Siberian tundra because they did achieve a higher intake rate during foraging than shorebird chicks in temperate agricultural grasslands. The much less dense vegetation of the tundra could play a major role in this, by making arthropods more easily detectable (less vegetation needs to be searched to find a prey item) or captured (less physical obstruction to moving chicks) than in temperate grassland swards. It is

FIGURE 9.4. Size distribution of birds breeding in high-arctic tundra in relation to feeding mode and chick diet. A: Number of species with breeding range extending into the circumpolar high-arctic tundra (based on Sale 2006). B: Mean percentage of total bird biomass for the three sites in fig. 9.3. Species exploiting marine food resources are not represented.



a challenge for future students to make comparative field measurements of intake rates of shorebird chicks in arctic and temperate environments, for instance using enclosures like those employed in chapters 5 and 6.

Small invertebrates constitute the main food base for non-herbivorous birds in arctic tundra. With the exception of cranefly larvae and earthworms that must be probed for, the great majority of these invertebrates have a dry mass of less than 3 mg, and beyond the size of adult craneflies (*c.* 12 mg) there is little to eat without switching to vertebrate prey. The numerous lemmings thus form the staple diet of most larger tundra predators. In some areas leftover berries from previous seasons provide a food source for ptarmigan, skuas, Sandhill Crane *Grus canadensis* and some adult shorebirds. As discussed above, self-feeding precocial development is well-suited to the exploitation of small food items, and this may help explain the proportional abundance of shorebirds in tundra bird communities. A score of altricial bird species also breed in arctic tundra – sometimes in considerable densities – but apart from predatory birds these are all passerines not exceeding the size of a Shore Lark *Eremophila alpestris* (32 g); there are no arctic thrushes, starlings or meadowlarks (fig. 9.4). In contrast, high-arctic shorebirds range from the 26 g Little Stint *Calidris minuta* to the 230 g Grey Plover *Pluvialis squatarola*, and their upper size limit may be set by the time needed to complete reproduction as much as by the size of tundra invertebrates (Visser 1991). Several arctic tundra sites provide an exciting opportunity to compare the reproductive energetics and foraging behaviour of altricial passerines with that of both similar-sized and larger precocial shorebirds utilizing the same (measurable) food base, and test the hypothesis that the costs of food transport to chicks limit the size distribution of parent-fed birds to smaller sizes than self-feeding species.

An alternative, though not exclusive, explanation that has been proposed for the relative abundance of shorebirds in arctic tundra is that the scarcity of pathogens and parasites in arctic regions allows chicks to economise on the development of a costly immune system and reallocate the energy thus saved to growth, but only if the birds can live in parasite-poor environments also during the part of the annual cycle spent away from the Arctic (Piersma 1997, Mendes *et al.* 2005). This proviso offers an explanation why shorebirds and seabirds which use marine habitats (which are 'healthy' as well) during migration and in winter, are plentiful in arctic tundra compared to freshwater species and landbirds. However it does not explain why all tundra-breeding shorebird species have self-feeding chicks.

PRECOCIAL PROBLEMS IN MODERN FARMLAND

From natural habitats to agricultural grasslands

At temperate latitudes, peat bogs and natural grasslands (which bear similarities to the arctic tundra in vegetation structure and available food types) formed the natural habitat of several shorebird species. When man created extensive agricultural grasslands, these were quickly colonised, leading to the bird community now known as 'meadowbirds' in lowland western Europe. Beintema *et al.* (1995, 1997) have pointed out that the colonisation of these grasslands, as they were gradually more intensively drained and fertilised to improve agricultural production, occurred in increasing order of species' body size. Beintema hypothesised that an associated increase in the abundance of large soil invertebrates (notably earthworms) enabled larger adult shorebirds to quickly collect the nutrients needed for a breeding attempt. On the other side of the coin, intensification also led to earlier and more frequent mowing and intensive grazing, reducing the perspectives for successfully raising chicks. Eventually these negative effects started to outweigh the benefits of intensification, and population declines ensued. The smaller species started to decline first because their lower adult survival rate at an identical clutch size (most shorebirds lay four eggs) renders their population dynamics more sensitive to reproductive losses, and because their later breeding phenology overlapped sooner with the advancing mowing dates (Beintema *et al.* 1995, 1997). Snipe, and to a lesser extent Ruff, are also more sensitive to drainage (Green 1988).

Interestingly, the increase in the availability of earthworms and other soil macroinvertebrates with intensification of agricultural grasslands was probably reversed in above-ground invertebrates. Several studies suggest that increases in fertiliser application and farming intensity lead to a reduction in the average size and size distribution of grassland arthropods, both in surface- and vegetation-dwelling taxa (Kajak 1978, Siepel 1990, Blake *et al.* 1994, Britschgi *et al.* 2006). The still limited data available suggest that the major shift in size distribution of grassland arthropods may have occurred already in the earlier stages of agricultural intensification, at fertiliser levels below those usually found within the intensity range of present-day Dutch farmland (Chapter 6, Siepel 1990, Kleijn *et al.* 2007). A reduction of the energetic profitability of prey items will reduce the intake rate of foraging insectivores even if total biomass is unaffected or increases. This could mean that larger shorebird chicks encounter the limits of an exploitable prey size distribution in agricultural grasslands, at intensification levels where food is not limiting for adults. The foraging observations described in chapter 5, combined with data on energy requirements (Chapter 2) and the size distribution of grassland invertebrates (Chapter 6) suggest that this is indeed the case in Black-tailed Godwits. Beintema *et al.* (1991) hypothesised that godwit chicks may escape this limitation by shifting to a diet of soil fauna as they grow larger, but our observations suggest that this happens only after fledging, when the chicks are approximately one month old. Without such an escape route, a reduction of average prey size will increase the time needed to fulfil the chick's daily energy needs, and render it vulnerable to variations in weather conditions and prey abundance. It would be interesting to obtain data on the size-density distribution of above-ground arthropods and the diet of godwit chicks in their original habitats, wet moorland, bogs and natural grasslands along lakes and rivers. This could even shed a new light on the conservation value for this species of seminatural habitats and grasslands managed to conserve botanical values, which are often considered unimportant for shorebirds due to a low availability of soil fauna for adults.

As small birds will less quickly run into prey size limitations than larger ones, a decreasing size of grassland arthropods with agricultural intensification is less likely to have affected chicks of the smaller shorebird species. However, an intriguing possibility is that such a reduction has contributed to the decline of altricial meadowbirds, because their sensitivity to prey size is increased by the need to transport food to the young (fig. 9.2). Grassland passerines like Skylark *Alauda arvensis*, Meadow Pipit *Anthus pratensis* and Yellow Wagtail *Motacilla flava* have shown declines that started at least as early and have been at least as strong as those of shorebirds (Bijlsma *et al.* 2001, Donald *et al.* 2001, Teunissen & Soldaat 2006), and a species like Whinchat *Saxicola rubetra* and Red-backed Shrike *Lanius collurio* have vacated Dutch farmland altogether. The simple model depicted in figure 9.2 suggests that birds as small as these can get into trouble at the average prey sizes available in modern grasslands (average *c.* 0.5 mg, few animals ≥4 mg, Chapters 5 and 6). Britschgi *et al.* (2006) showed how Whinchats breeding in intensively farmed alpine meadows deliver smaller arthropods to their young though at the same rate as in less intensively used fields (where available prey were larger), leading to a reduction in nestling survival.

Factors affecting chick survival in farmland

Since the 1950s and 1960, the populations of most meadowbird species have shown severe declines in the Netherlands. The total area of grassland has declined by some 26% over this period (Statstics Netherlands, Statline), due to urbanisation and conversion to arable land. Additional grassland area has become unsuitable for breeding as a result of disturbance zones around the increasingly dense network of roads, railways, tree lines, farms and other buildings. The intensive use of farmland put the breeding success of birds in the remaining areas under pressure. Earlier dates of mowing and grazing and increased stocking rates reduced clutch survival (Beintema & Müskens 1987). However, the compilation of breeding success estimates for Black-tailed Godwits presented in figure 7.4 suggests that chick survival has declined even more strongly. In combination with the observation that survival of adult godwits does not seem to have declined or been consistently low in recent decades (Roodbergen *et al.* subm.), this indicates that the main causes of the species' ongoing population decline must be sought in a failure to produce sufficient fledged young. A similar population decline driven by declining productivity rather than reduced adult survival has been reported for Northern Lapwings in Britain (Peach *et al.* 1994, Besbeas *et al.* 2002). In both godwits and lapwings, breeding output is more sensitive to factors affecting chick survival than to clutch survival (Schekkerman *et al.* 2005, Teunissen *et al.* 2005b), as lost clutches are often replaced, but the death of a brood is usually not. Thus, it is important to direct research and conservation actions towards the survival of chicks. This applies particularly to Black-tailed Godwits, whose chicks are most sensitive to grassland management because of their feeding habits and preference for tall, uncut swards.

In chapter 1, a hypothetical model was presented of how grassland management, weather conditions and predation may in concert influence the growth and survival of grassland shorebird chicks. Through the work presented in the previous chapters, we are now able to quantify many of these relationships for Black-tailed Godwits (fig. 9.5). In chapter 2, we measured the amount of energy metabolised by chicks at different body masses. Both Daily Energy Expenditure (DEE) and total Daily Metabolised Energy (DME, including energy incorporated in tissues) increased proportional to chick mass. These measurements also showed that increased expenditure on thermoregulation and activity occurred at the expense of growth rate. Weather affects not only energy

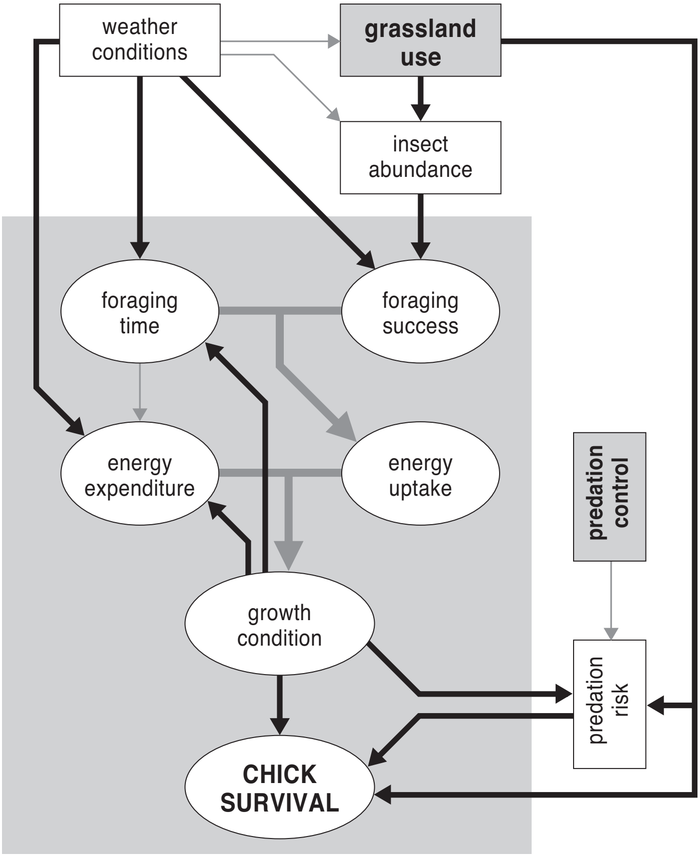


FIGURE 9.5. Schematic representation of relationships between environmental conditions (weather, grassland use and predation) and the growth and survival of black-tailed godwit chicks (represented by the shaded rectangle). Black arrows denote relationships confirmed and quantified in this thesis; thin grey arrows relationships that have not been addressed. Thick grey arrows denote relationships that can be derived from first principles.

expenditure but also energy uptake of godwit chicks, because low temperature and rainfall increased the time that chicks spend being brooded, and because their foraging success is reduced at higher wind speeds (Chapter 5). Weather is also likely to influence the abundance of food for chicks through effects on arthropod emergence and reproduction, but we did not address this in our studies. We did investigate the effect of agricultural grassland management on insect abundance, and found both a strong immediate negative effect of mowing and indications for a longer-term reduction in fields used for commercial dairy farming compared to a less intensively used meadowbird reserve. The mowing effect translated into a 31% lower foraging success of godwit chicks (Chapter 6). Unless foraging time can be increased (but the scope for that is very limited, Chapter 5), this would mean a reduction in energy intake of a similar magnitude as the amount of energy normally allocated to growth (Chapter 2), and lead to a strong reduction in growth rate and body condition. A decline in condition feeds back to foraging time via an increase in brooding time, but we found no effect of condition on foraging success (Chapter 5).

If sustained over a longer period, a reduction in growth rate can result in death. Both the distribution of body masses of chicks encountered alive and those of radio-tagged chicks that were found dead under conditions suggesting starvation indicate that this happens at a condition index of 0.4-0.6, i.e. when the chick weighs only half as much as expected at its age. However, before that time chicks may fall victim to a plethora of other mortality factors, the likelihood of some of which may also depend on their condition. In chapter 8 we found that predation (possibly confounded with a limited amount of scavenging) was the most frequent cause of death of chicks, and predators are likely to remove many chicks before they starve to death. Indeed we observed that the probability for godwit chicks to die of causes other than obvious starvation increased at low condition indices, probably mainly due to predation. We also found that predation risk is affected by the agricultural use of grassland: godwit chicks staying in recently cut or grazed fields with a short sward were more likely to be taken, especially by avian predators, than chicks staying in the uncut, taller swards which they prefer (Chapter 8). Finally, agricultural use of grasslands also affects chick mortality directly: chicks are killed during cutting and harvesting of grass, and they drown in ditches if the sides are too steep to climb (Chapter 8).

It would be presumptuous to state that we now have a complete understanding of the factors influencing growth and survival of godwit chicks in agricultural grasslands, but at least we know for most of them the direction in which they operate, and have an idea of their quantitative strength. The next step towards a fuller understanding is to use the relationships quantified in this thesis to construct a simulation model for chick growth and survival. Exploring various environmental scenarios with such a model will help us disentangle the relative importance of different environmental factors. It is also one of the few ways open to predict the joint effect of changes that affect chicks via multiple pathways. Examples are the feedback of a poor body condition on chick performance, and the effects of climate change. While a change in spring weather patterns will obviously affect the chicks' energy expenditure, it will also affect energy uptake either directly through brooding time and foraging success or indirectly through changes in the abundance and phenology of grassland arthropods. Moreover, farming practice will also adapt to the new climate regime, and this will impact on food availability, mowing mortality and predation risk. It is therefore important to include effects of weather on agricultural grassland use in a model of chick growth and survival (fig. 9.5). Based on the work described here, Teunissen *et al.* (2008) describe the parameterisation of such a model.

The roles of farming and predation

In the foregoing, grassland use (particularly mowing schedules), predation and weather were identified as the main factors affecting the growth and fledging success of godwit chicks. The relative effect of each of these factors is a matter of concern, because this impinges on the effectiveness of conservation strategies. Various chapters of this thesis appear at first sight to present conflicting evidence on this. The data on arthropod abundance and chick foraging success in cut and uncut grasslands (Chapter 6), in combination with those on energy budgets (Chapter 2), suggest that intensive dairy farming does create significant food availability problems for chicks. On the other hand, the telemetry studies indicated that predation is a far more frequent cause of death of chicks than mowing or starvation (Chapter 8), even if measurable interactions between predation and agriculture are taken into account. However, the telemetry studies also showed that when different sites are compared, the survival of godwit chicks is positively correlated with the availability of uncut and other tall grassland during the prefledging period (Chapter 7).

Predation is a process that is hard to study because it is seldom witnessed directly. The use of radio transmitters has greatly helped us unveil some of its features, but the fact that broods are quite mobile but were relocated at intervals much longer than the timescale of a predation event is likely to have limited the resolution with which we could detect potentially important interactions. An interaction that is hard to quantify arises through negatively density-dependent predation: a declining breeding density (due to intensive farming) reduces the ability of meadowbirds to cooperatively evict potential predators (Green *et al.* 1990, Berg *et al.* 1992, Teunissen *et al.* 2005b). On the other hand, it would be almost surprising if the (re)invasion of farmland by generalist predators like the Common Buzzard would not have consequences for some prey populations, particularly in a landscape where their reproductive success is already severely under pressure.

In 2006, the year after the completion of the studies described here, unusually cold weather in March and early April slowed down vegetation development in grasslands throughout the Netherlands. After a warm spell followed a three-week rainy period in May, and the majority of meadows was not cut until early June, at least three weeks later than usual and reminiscent of mowing dates that were usual half a century ago (*cf.* fig. 9.6a). An index of breeding success based on counts of alarming pairs in the main fledging weeks of chicks in the province of Friesland was significantly higher in 2006 than in the preceding nine years for both Black tailed Godwit and Redshank (Nijland 2007). Similarly favourable results were observed elsewhere in the Netherlands (Teunissen *et al.* 2007). For the first time in ten years, reproductive success may have been high enough to compensate adult mortality in many conventionally farmed areas. Evidently, effects of grassland condition and management can overrule those of variation in weather conditions and predation pressure.

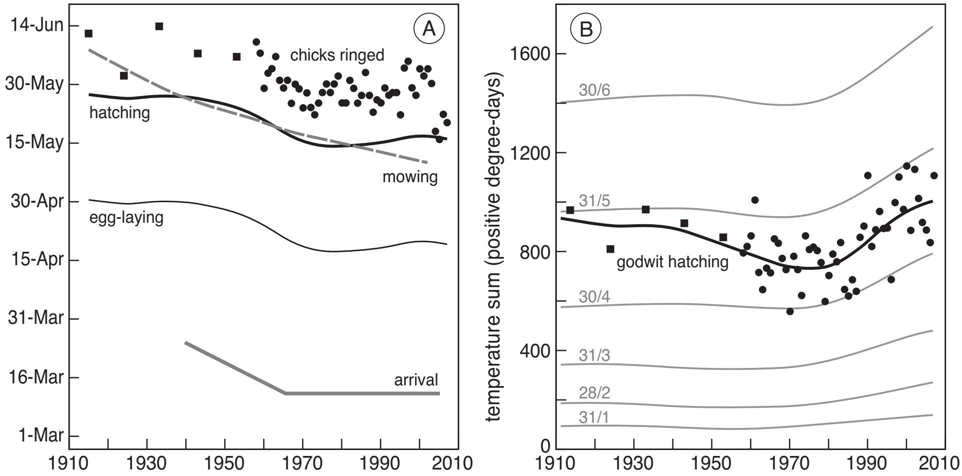
Do godwits track changes in farming and climate?

Within a breeding season, the relatively late-laying pairs within the meadowbird population are likely to suffer most from the effects of modern farming practice, as their eggs and chicks are more likely to be confronted with cutting or grazing and the area of suitable chick foraging habitat diminishes. Hatching success of meadowbird clutches declines in the later part of the nesting season (Beintema & Müskens 1987, Teunissen *et al.* 2005b), and fledging success of godwit chicks also declines in the course of the spring (Teunissen *et al.* 2008, Roodbergen & Klok in press). Roodbergen & Klok (in press) found that the earliest-laying godwit pairs fledge 2-3 times as many chicks than late-laying pairs in the same sites. A farming-induced reduction in reproductive output of late-breeding pairs is expected to lead to selection for breeding earlier. By analysing the dates on which chicks were ringed in the Netherlands, Beintema *et al.* (1985) showed that the median hatching date of grassland shorebirds has indeed advanced by two to four weeks between 1911 and 1970. An extension of this analysis for Black-tailed Godwits is presented in fig. 9.6. The data suggest that godwit laying dates may not have changed systematically before 1950, perhaps because agricultural practice at that time did not yet curtail the breeding success of late pairs. Information on population trends (fig. 1.2) suggests that intensification started to negatively affect godwits sometime in the 1950s or early 1960s, and this coincides with the time that godwit laying dates started to change. The birds seem to have tracked changes in (estimated) date of the first grassland cut fairly closely until about 1970. Since then however, godwits have not advanced their breeding season any further (fig. 9.6a). This is supported by median hatching dates estimated independently (from the incubation stage of clutches) in 24 sites in 1997-2006 (Teunissen *et al.* 2008): the medians (19 May in the North and 11 May in the West of the country), are very close to median dates reported for 1976-85 (18 May in Friesland and 13 May elsewhere, Beintema 1995). In the same period, mowing dates have continued to advance, and most godwit chicks nowadays hatch after the date on which 50% of the agricultural grasslands have been mown (fig. 9.6a).

Some factor thus must have counteracted selection for breeding earlier since the 1970s. Stabilising pressures may arise from limits to the ability of birds to advance their arrival dates (Both *et al.* 2005a), nutritive or energetic problems for females to produce eggs earlier in the spring (Perrins 1970, Högstedt 1974, Nager 2006), a higher predation rate on nests in short vegetations (Beintema & Müskens 1987), or a reduced survival of chicks born early, in colder weather (Beintema & Visser 1989). Climate may influence most of these factors. Temperature sums are often good predictors of phenology of plants and animals, including between-year variation in laying dates of Black-tailed Godwits (Kruk *et al.* 1996). The development of temperature sums during spring in the Netherlands remained constant in the first half of the 20th century, was somewhat retarded in the 1960s and 1970s, and thereafter has shown a rapid acceleration, especially since the late 1980s (fig. 9.6b). Godwit laying dates advanced during the period of slight climatic cooling in the 1950s and 1960s, and occurred at progressively lower temperature sums (fig. 9.6b). Hence, the driver of this advance is unlikely to have been climate warming, as proposed for Northern Lapwings by Both *et al.* (2005b). Both mowing grassland (by farmers) and finding suitable nesting sites providing concealment (by godwits) became possible at lower temperature sums as intensive drainage and fertilisation of fields accelerated development of the grass sward. Fertilisation will also have reduced limitations for the godwits to accumulate nutrients for a clutch through an increase of soil invertebrates (Högstedt 1974, Wymenga & Alma 1998).

After *c.* 1980, the advancement of godwit laying dates on temperature sums has been reversed into a strong delay (fig. 9.6b).This cannot be explained by pre-laying females expending more energy or by chicks surviving less well in cold early spring weather, as both these potentially stabilising factors have weakened. This points to problems associated with producing eggs earlier in the season. As far as the scant data

FIGURE 9.6. Changes in the phenology of breeding season events in Black-tailed Godwits in the past century (A) in relation to the development of spring temperatures (B). In panel A, black symbols show the median ringing dates of chicks in the Netherlands (squares are means over 6-12 year periods as given by (Beintema *et al.* 1985) (N=18-582 chicks per period); dots are annual data from database of Dutch Centre for Avian Migration and Demography (N=125-1632 chicks per year, available from 1958 onwards). To estimate hatching dates from these data, the median hatching date reported by (Beintema 1995) for 1976-1985 was subtracted from the median ringing date in those same years to obtain the average age at ringing (13 days), which was assumed to have remained constant over time until 2002. In 2003-2006 intensive radiotelemetry studies (Chapters 7 & 8) sought to ring chicks directly after hatching, and average age at ringing was 4 days. The bold black line is a smoothing spline (5 d.f.) through the estimated hatching dates; assuming no significant change in the frequency of replacement clutches this reflects the median start of egg-laying 27 days earlier (thin black line). Approximate peak arrival dates (thick grey line) are based on (Mulder 1972) for the 1930s and 1960s, and on first spring resightings of godwits colour-ringed in the W Netherlands for 2004-2007 (own unpubl. data). Dates of first grass cut (broken grey line) follow (Beintema et al. 1985) for 1910-1970, and own observations in 1997-2005 (24 site/year combinations, Teunissen *et al.* 2008). In panel B, the development of winter and spring climate is shown as temperature sums (accumulated positive daily average temperatures since 1 January, data KNMI, De Bilt) at the end of each month (grey smoothing splines, 5 d.f.). Temperature sums on the median hatching date of godwit chicks (from A) are shown by dark grey symbols and a black smoothing spline (5 d.f.).



indicate, arrival dates of godwits in the Netherlands seem to have advanced and then stabilised roughly in parallel with laying dates (fig. 9.6a), suggesting an invariant pre-laying interval for which we must find an explanation. The risk of arriving in freezing conditions that render food inaccessible has decreased as winters have become milder, but there may be other factors that counteract an earlier departure from the African wintering grounds or migratory stopover sites in southern Europe. The use of stopover sites in late winter and spring by Black-tailed Godwits of the nominate subspecies seems to have changed over the past decades, but much is still unclear about this (Gill *et al.* 2008). The long interval between the arrival date of the majority of adults in the Netherlands and the onset of laying (*c.* 6 weeks, fig. 9.6a) suggests that the nutrients incorporated in eggs may be collected mainly after arrival on the breeding grounds. Foraging conditions in this period may thus be critical, but during the early weeks of their stay in the Netherlands, godwit flocks do not seem particularly food-stressed, taking considerable time to rest, preen and socialise (Lesseliers 2002). To better understand the lack of response of Black-tailed Godwit phenology to environmental change, we clearly need more research into their migratory stopover ecology and into foraging conditions and energetics during the period between arrival and laying.

In contrast to Black-tailed Godwits, Dutch farmers have been able to track the recent advancement of spring climate; the first grassland cut is made at roughly the same temperature sum nowadays as in the 1980s (Teunissen *et al.* 2008). That the hatching date of chicks has not advanced in parallel means not only that yet less uncut grassland is available for them as foraging habitat, but also that the vegetation on those remaining fields is in a more advanced stage of growth; approximately 250 degree-days more have accumulated when chicks hatch now than 25 years ago. This results in a higher and denser sward, an effect additional to the increase in vegetation density that is the result of fertilisation and grassland improvement (Teunissen *et al.* 2008). Tall dense swards present a larger volume of vegetation to be searched and are likely to be penetrated less easily by foraging chicks (Kleijn *et al.* 2007). It is doubtful that this is balanced by a matching increase in invertebrate abundance, not in the least because the phenology of arthropods may also have shifted. The net energy intake of chicks and hence the quality of uncut grassland as foraging habitat thus have probably declined. Further work is clearly needed to quantify the effects of sward structure and composition on chick foraging conditions.

A conservation strategy for Black-tailed Godwits

The combined results presented in this thesis indicate that intensification of agricultural grassland use, particularly the advancement of mowing dates, is a major factor reducing the reproductive output of Black-tailed Godwits. At the same time however, other factors have changed as well, including spring phenology, floral composition of grasslands and the (renewed) presence of chick predators in the meadowbird landscape. A consequence of these accumulated changes is that relatively simple measures like nest protection and postponing mowing dates no longer suffice to restore conditions for chick survival to those prevailing a few decades ago. The results of our study into the effectiveness of mosaic management (Chapter 7) point in this direction: godwit chick survival was enhanced by mowing more grassland late, but it did not result in a sufficiently high breeding productivity in the managed sites. This result adds on to other recent studies into the effectiveness of agri-environment schemes for meadowbirds in the Netherlands, that found that densities of breeding birds on fields with agri-environment contracts did not differ from controls (Kleijn *et al.* 2001) or where densities differed these probably existed already at the onset of management (Kleijn & van Zuijlen 2004, Verhulst *et al.* 2007), and that the initiation of contracts did not lead to a more positive population development (Willems *et al.* 2004). Most of the practical measures included in these schemes have been shown or are likely to benefit clutches or chicks in some way (Beintema & Müskens 1987, Kruk *et al.* 1997, Teunissen 2000, Schekkerman & Müskens 2001, Oosterveld *et al.* 2008, Chapters 6-8) but evidently they are applied with insufficient intensity (e.g. a too small proportion of fields mown late) or their effectiveness is negated by other factors. To be successful on the long term, measures will thus have to be intensified, and at the same time made more comprehensive in order to reduce any additional limitations. For instance, it should be ensured that fields with a postponed mowing date have a suitable vegetation structure at the time that chicks need them; this can be done either by setting entry criteria (e.g. floral composition, contract duration) or changing prescriptions (e.g. limit fertiliser input, groundwater table). This greater restrictiveness will reduce the attractiveness of joining the scheme to farmers, and increase the level of financial compensation required for those that do. Large-scale employment of such far-reaching measures across the Dutch farmland is therefore not very likely to find enough support and financial resources. The most effective strategy will then be to concentrate conservation efforts in those areas with favourable environmental preconditions (including landscape structure, water tables, predation, disturbance etcetera) and apply intensive measures here. By optimising all (or most) environmental variables simultaneously, either by choice of location or by management, the effectiveness of measures will be enhanced, and the requirement that breeding productivity is high enough for meadowbird populations to sustain themselves is most likely to be fulfilled. It is also both more feasible and more defensible to implement predation control (if at all necessary) in restricted areas where other limitations have been lifted than throughout the rural countryside (Teunissen *et al.* 2005b, Bolton *et al.* 2007).

Such a strategy may seem like abandoning the Black-tailed Godwits still persisting at lower densities elsewhere to their fate, but the data on reproductive success suggest that many of these populations have a poor chance of surviving in the continuously changing Dutch farmland. Perspectives for a halt or reversal of agricultural intensification are poor, unless drastic changes in the European Common Agricultural Policy divert significant financial incentives away from agricultural production to maintenance and development of landscape and natural values (Donald *et al.* 2001, Donald *et al.* 2006, Wretenberg *et al.* 2007). It does not necessarily mean that no godwit populations can persist outside the core areas; depending on their size and quality the latter may produce a surplus of recruits sustaining low densities in the wider countryside. Neither does it mean that farmers have no part to play in meadow bird conservation. 'Easy' measures (including nest protection, refuge strips, scaring birds off fields before mowing, mowing centrifugally, and in daytime only) should still be applied outside the core areas, if only to benefit species other than Black-tailed Godwits and to comply to existing legislation. Moreover, management in the core areas needs not be delegated solely to nature conservation organisations. Given the diverse requirements of different meadowbird species and age-classes, a spatial combination of different types of land-use is called for and this can at least in part be implemented by farmers also reaping economic benefits from agricultural production. The requirement is that conservation is the leading principle in management decisions, and that the financial resources to make this possible are available.

Recently, the Dutch government has reviewed its policy for meadow bird conservation and made adjustments in this direction (Laporte & de Graaff 2006). Conservation efforts will be concentrated in an area of 280,000 ha, to be selected on the basis of actual or potential meadow bird densities, and implemented via 'area plans' developed jointly by multiple organisations involved in regional management. Whether these changes will be successful will depend on their implementation, which is still in its infancy. Key issues will be the success in delineating and protecting the most suitable areas and organising the coordinated management of important environmental variables here, and whether it will be possible to sufficiently change grassland use and quality. Taking account of the measures included in some of the schemes being developed under the new policy, it seems that there still is a long way to go. The target area of 280,000 ha for the new policy was based on an estimate of the land surface needed to accomodate a population of *c.* 50,000 godwit pairs, and amounts to 28% of the total Dutch grassland area and 75% of the area where densities of 5 godwit pairs/ha still occur (Teunissen *et al.* 2005a). However, the criterium should be to maximise the size of meadowbird populations that achieve sufficiently high reproductive success to balance mortality. In the long run properly conserving a smaller population will be more effective than spreading the same budget across insufficiently intense measures in a large area.

REFERENCES

- Anava A., M. Kam, A. Shkolnik & A.A. Degen 2001. Growth rate and energetics of Arabian Babbler (*Turdoides squamiceps*) nestlings. Auk 118: 519-524.
- Andreev A.V. 1999. Energetics and survival of birds in extreme environments. Ostrich 70: 13-22.
- Beale C.M., S. Dodd & J.W. Rearce-Higgins 2006. Wader recruitment indices suggest nesting success is temperature-dependent in Dunlin *Calidris alpina*. Ibis 148: 405-410.
- Beintema A.J., R.J. Beintema-Hietbrink & G.J.D.M. Müskens 1985. A shift in the timing of breeding in meadow birds. Ardea 73: 83-89.
- Beintema A.J. & G.J.D.M. Müskens 1987. Nesting success of birds breeding in Dutch agricultural grasslands. Journal of Applied Ecology 24: 743-758.
- Beintema A.J. & G.H. Visser 1989. Growth-parameters in chicks of Charadriiform birds. Ardea 77: 169-180.
- Beintema A.J., J.B. Thissen, D. Tensen & G.H. Visser 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. Ardea 79: 31-43.
- Beintema A.J. 1995. Fledging success of wader chicks, estimated from ringing data. Ringing & Migration 16: 129-139.
- Beintema A.J., O. Moedt & D. Ellinger 1995. Ecologische atlas van de Nederlandse weidevogels. Schuyt & Co, Haarlem.
- Beintema A.J., E. Dunn & D. Stroud 1997. Birds and wet grasslands. In: D.J. Pain & M.D. Pienkowski (eds.) Farming and birds in Europe: the Common Agricultural Policy and its implications for bird conservation: 269-296. Academic Press, San Diego.
- Berg, A. T. Lindberg & K.G. Kallebrink 1992. Hatching success of Lapwings on farmland: differences between habitats and colonies of different sizes. Journal of Animal Ecology 61: 469-476.
- Besbeas P., S.N. Freeman, B.J.T. Morgan & E.A. Catchpole 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58: 540-547.
- Bijlsma R., F. Hustings & C.J. Camphuysen 2001. Common and scarce birds of The Netherlands. Avifauna of the Netherlands 2. GMB / KNNV, Haarlem.
- Blake S., G.N. Foster, M.D. Eyre & M.L. Luff 1994. Effects of habitat type and grassland management-practices on the body-size distribution of Carabid beetles. Pedobiologia 38: 502-512.
- Boertmann D., H. Meltofte & M. Forchhammer 1991. Population densities of birds in central northeast Greenland. Dansk Ornithologiske Forenings Tidsskrift 85: 151-160.
- Bolton M., G. Tyler, K. Smith & R. Bamford 2007. The impact of predator control on Lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. Journal of Applied Ecology 44: 534-544
- Both C., R.G. Bijlsma & M.E. Visser 2005a. Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. Journal of Avian Biology 36: 368-373.
- Both C., T. Piersma & S.P. Roodbergen 2005b. Climatic change explains much of the 20th century advance in laying date of Northern Lapwing *Vanellus vanellus* in The Netherlands. Ardea 93: 79-88.

- Britschgi A., R. Spaar & R. Arlettaz 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: lessons for overall Alpine meadow management. Biological Conservation 130: 193-205.
- Bryant D.M. & P. Tatner 1991. Intraspecies variation in avian energy-expenditure - correlates and constraints. Ibis 133: 236-245.
- Carey C. 1986. Avian reproduction in cold climates. In: H. Ouellet (ed.) Acta XIX Congressus Internationalis Ornithologici, Ottawa, Ontario, 1986: 2708-2715. National Museum of Natural Sciences, Ottawa.
- Danks H.V. 1999. Life cycles in polar arthropods - flexible or programmed? European Journal of Entomology 96: 83-102.
- Degen A.A., B. Pinshow, R. Yosef, M. Kam & K.A. Nagy 1992. Energetics and growth-rate of Northern Shrike (*Lanius excubitor*) nestlings. Ecology 73: 2273-2283.
- Donald P.F., R.E. Green & M.F. Heath 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London Series B 268: 25-29.
- Donald P.F., F.J. Sanderson, I.J. Burfield & F.P.J. van Bommel 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. Agriculture Ecosystems & Environment 116: 189-196.
- Drent R.H., M. Klaassen & B. Zwaan 1992. Predictive growth budgets in terns and gulls. Ardea 80: 5-17.
- Fortin D., G. Gauthier & J. Larochelle 2000. Body temperature and resting behavior of Greater Snow Goose goslings in the high Arctic. Condor 102: 163-171.
- Gabrielsen G.W., M. Klaassen & F. Mehlum 1992. Energetics of Black-legged Kittiwake *Rissa tridactyla* chicks. Ardea 80: 29-40.
- Gill J.A., R.H.W. Langston, J. Alves, P.W. Atkinson, P. Bocher, N.C. Vieira, N.J. Crockford, G. Gélinaud, N. Groen, T.G. Gunnarsson, B. Hayhow, J. Hooijmeier, R. Kentie, D. Kleijn, P. Lourenço, J.A. Masero, F. Meunier, P.M. Potts, M. Roodbergen, H. Schekkerman, E. Wymenga & T. Piersma 2008. Contrasting populations trends in two populations of black-tailed godwit, Limosa limosa: a review of causes and recommendations. Wader Study Group Bulletin in press.
- Green R.E. 1988. Effects of environmental factors on the timing and success of breeding of Common Snipe *Gallinago gallinago* (Aves, Scolopacidae). Journal of Applied Ecology 25: 79-93.
- Green R.E., G.J.M. Hirons & J.S. Kirby 1990. The effectiveness of nest defense by Black-tailed Godwits *Limosa limosa*. Ardea 78: 405-413.
- Hodum P.J. 2002. Breeding biology of high-latitude Antarctic fulmarine petrels (Procellariidae). Journal of Zoology 256: 139-149.
- Hodum P.J. & W.W. Weathers 2003. Energetics of nestling growth and parental effort in Antarctic fulmarine petrels. Journal of Experimental Biology 206: 2125-2133.
- Högstedt G. 1974. Length of the pre-laying period in the Lapwing *Vanellus vanellus* L. in relation to its food resources. Ornis Scandinavica 5: 1-4.
- Janes D.N. 1997. Energetics, growth, and body composition of Adelie penguin chicks, Pygoscelis adeliae. Physiological Zoology 70: 237-243.

- Joest R. 2003. Junge Säbelschnäbler (*Recurvirostra avosetta* L.) in unterschiedlichen Klimazonen: Physiologische und ethologische Anpassungen an Ökologische Bedingungen in Norddeutschland und Südspanien. PhD Thesis, Christian-Albrechts-Universität, Kiel.
- Kajak A. 1978. The effect of fertilizers on numbers and biomass of spiders in a meadow. Symposia of the Zoological Society of London 42: 125-129.
- Klaassen M. & R. Drent 1991. An analysis of hatchling resting metabolism - in search of ecological correlates that explain deviations from allometric relations. Condor 93: 612-629.
- Klaassen M. 1994. Growth and energetics of tern chicks from temperate and polar environments. Auk 111: 525-544.
- Klaassen M., B. Habekotte, P. Schinkelshoek, E. Stienen & P. Van Tienen 1994. Influence of growth-rate retardation on time budgets and energetics of Arctic Tern *Sterna paradisaea* and Common Tern *S. hirundo* chicks. Ibis 136: 197-204.
- Kleijn D., F. Berendse, R. Smit & N. Gilissen 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413: 723-725.
- Kleijn D. & G.J.C. van Zuijlen 2004. The conservation effects of meadow bird agreements on farmland in Zeeland, The Netherlands, in the period 1989-1995. Biological Conservation 117: 443-451.
- Kleijn D., W. Dimmers, R. van Kats, D. Melman & H. Schekkerman 2007. De voedselsituatie voor weidevogelkuikens bij agrarisch mozaiekbeheer. Alterra-rapport 1487, Alterra, Wageningen UR.
- Konarzewski M., J.R.E. Taylor & G.W. Gabrielsen 1993. Chick energy requirements and adult energy expenditure of Dovekies (*Alle alle*). Auk 110: 343-353.
- Krijgsveld K.L., J.M. Olson & R.E. Ricklefs 2001. Catabolic capacity of the muscles of shorebird chicks: maturation of function in relation to body size. Physiological and Biochemical Zoology 74: 250-260.
- Kruk M., M.A.W. Noordervliet & W.J. ter Keurs 1996. Hatching dates of waders and mowing dates in intensively exploited grassland areas in different years. Biological Conservation 77: 213-218.
- Kruk M., M.A.W. Noordervliet & W.J. ter Keurs 1997. Survival of black-tailed godwit chicks Limosa limosa in intensively exploited grassland areas in The Netherlands. Biological Conservation 80: 127-133.
- Kvist A. & A. Lindström 2000. Maximum daily energy intake: It takes time to lift the metabolic ceiling. Physiological and Biochemical Zoology 73: 30-36.
- Lack D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Laporte G. & R.P.M. de Graaff 2006. Een Rijk Weidevogellandschap: actieprogramma van het Weidevogelverbond. WING Process Consultancy, Wageningen.
- Lesseliers H. 2002. Telling van Grutto's *Limosa limosa* tijdens het voorjaar (1997-2001) in het Turnhouts Vennengebied: relatie tussen verzamelplaats en broedgebied. Natuur Oriolus 68: 37-46.
- Maclean S.F. & F.A. Pitelka 1971. Seasonal patterns of abundance of tundra arthropods near Barrow. Arctic 24: 19-&.
- Mendes L., T. Piersma, M. Lecoq, B. Spaans & R.E. Ricklefs 2005. Disease-limited distributions? Contrasts in the prevalence of avian malaria in shorebird species using marine and freshwater habitats. Oikos 109: 396-404.

- Mock P.J., M. Khubesrian & D.M. Larcheveque 1991. Energetics of growth and maturation in sympatric passerines that fledge at different ages. Auk 108: 34-41.
- Morrison R.I.G. 2004. Using migration counts from eastern Canada to access productivity of arctic-breeding shorebirds in relation to climate. Arctic Monitoring and Assessment Program report, 2004.
- Mulder T. 1972. De Grutto in Nederland. Wetenschappelijke Mededeling nr 90, KNNV, Hoogwoud.
- Nager R.G. 2006. The challenges of making eggs. Ardea: 323-346.
- Nijland F. 2007. Een succesvol broedjaar voor weidevogels in 2006. Limosa 80: 96-101.
- Obst B.S. & K.A. Nagy 1993. Stomach oil and the energy budget of Wilsons Storm-Petrel nestlings. Condor 95: 792-805.
- Oosterveld E.B., D. Kleijn & H. Schekkerman 2008. De invloed van beheer op de overlevingskansen van weidevogeljongen: kennisoverzicht en effectiviteit van maatregelen. A&W-rapport 995, Altenburg & Wymenga ecologisch onderzoek /Alterra /Vogeltrekstation, Veenwouden.
- Peach W.J., P.S. Thompson & J.C. Coulson 1994. Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. Journal of Animal Ecology 63: 60-70.
- Perrins C.M. 1970. Timing of birds' breeding seasons. Ibis 112: 242-255.
- Piersma T. 1997. Do global patterns of habitat use and migration strategics co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? Oikos 80: 623-631.
- Rasch M. & K. Caning 2004. Zackenberg Ecological Research Operations, annual report 2003, Danish Polar Center, Copenhagen.
- Ricklefs, R.E. & J.M. Starck 1998a. Embryonic growth and development. In: J.M. Starck & R.E. Ricklefs (eds.) Avian postnatal development: 31-58. Oxford University Press, New York.
- Ricklefs R.E. & J.M. Starck 1998b. The evolution of the developmental mode in birds. In: J.M. Starck & R.E. Ricklefs (eds.) Avian postnatal development. p 366-380. Oxford University Press, New York.
- Ricklefs R.E., J.M. Starck & M. Konarzewski 1998. Internal constraints on growth in birds. In: J.M. Starck & R.E. Ricklefs (eds.) Avian postnatal development: 266-287. Oxford University Press, Oxford.
- Roodbergen M., T.C. Klok & H. Schekkerman MS. Local adult survival and breeding site fidelity of Black-tailed godwits (*Limosa limosa*) in four local populations in the Netherlands in 2002-2005. Submitted manuscript.
- Roodbergen M. & C. Klok in press. Timing of breeding and reproductive output in the Black-tailed Godwit (*Limosa limosa*) at two study sites in the Netherlands. Ardea, in press.
- Roth T.C., J.A. Lesku, C.J. Amlaner & S.L. Lima 2006. A phylogenetic analysis of the correlates of sleep in birds. Journal of Sleep Research 15: 395-402.
- Sale R. 2006. A complete guide to arctic wildlife. Christopher Helm, London.
- Salomonsen, F. 1972. Zoogeographical and ecological problems in arctic birds. Proceedings International Ornithological Congress, 15: 25-77.
- Schekkerman H. & G. Müskens 2000. Produceren Grutto's *Limosa limosa* in agrarisch grasland voldoende jongen voor een duurzame populatie? Limosa 73: 121-134.

- Schekkerman H. & G.J.D.M. Müskens 2001. 'Vluchtstroken' als instrument in agrarisch weidevogelbeheer, Alterra, Wageningen.
- Schekkerman H. & G.H. Visser 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. Auk 118: 944-957.
- Schekkerman H., I. Tulp, T. Piersma & G.H. Visser 2003. Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. Oecologia 134: 332-342.
- Schekkerman H., W. Teunissen & E. Oosterveld 2005. Broedsucces van grutto's bij agrarisch mozaïekbeheer in 'Nederland Gruttoland'. Alterra-rapport 1291, Alterra, Wageningen.
- Siepel, H 1990. The influence of management on food size in the menu of insectivorous animals. . Proceedings in Experimental and Applied Entomology, N.E.V. Amsterdam 1: 69-74.
- Starck J.M. & R.E. Ricklefs 1998. Patterns of development: the altricial-precocial spectrum. In: J.M. Starck & R.E. Ricklefs (eds.) Avian growth and development: 3-31. Oxford University Press, New York.
- Tatner P. & D.M. Bryant 1993. Interspecific variation in daily energy expenditure during avian incubation. Journal of Zoology 231: 215-232.
- Temrin H. & B.S. Tullberg 1995. A phylogenetic analysis of the evolution of avian mating systems in relation to altricial and precocial young. Behavioral Ecology 6: 296-307.
- Teunissen W.A. 2000. Het effect van vrijwillige weidevogelbescherming op de aantalsontwikkeling en het reproductiesucces van weidevogels. SOVON-onderzoeksrapport 2000/04, SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Teunissen W.A., W. Altenburg & H. Sierdsema 2005a. Toelichting op de gruttokaart van Nederland 2004. SOVON-onderzoeksrapport 2005/04, SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Teunissen W.A., H. Schekkerman & F. Willems 2005b. Predatie bij weidevogels. SOVON-onderzoeksrapport 2005/11, SOVON, Beek-Ubbergen.
- Teunissen W.A. & L.L. Soldaat 2006. Recente aantalsontwikkeling van weidevogels in Nederland. De Levende Natuur 107: 70-74.
- Teunissen W. 2007. Afname van weidevogels versnelt sinds eeuwwisseling. SOVON-nieuws 20: 15-17.
- Teunissen W., F. Willems & F. Majoor 2007. Broedsucces van de Grutto in drie gebieden met verbeterd mozaïekbeheer. SOVON-onderzoeksrapport 2007/06, SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Teunissen W.A., C. Klok, D. Kleijn & H. Schekkerman 2008. Factoren die de overleving van weidevogelkuikens beïnvloeden. SOVON-onderzoeksrapport 2008-01, SOVON Vogelonderzoek Nederland/Alterra/Vogeltrekstation, Beek-Ubbergen.
- Thomas G.H. & T. Szekely 2005. Evolutionary pathways in shorebird breeding systems: sexual conflict, parental care, and chick development. Evolution 59: 2222-2230.
- Thomas G.H., R.P. Freckleton & T. Szekely 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. Proceedings of the Royal Society B 273: 1619-1624.
- Tinbergen J.M. & J.B. Williams 2002. Energetics of incubation. In: D.C. Deeming (ed.) Avian Incubation: 299-314. Oxford University Press, Oxford.
- Tjørve K.M.C. 2006. From an egg to a fledgling: a perspective on shorebird breeding ecology and chick energetics. PhD Thesis, University of Groningen, Groningen.

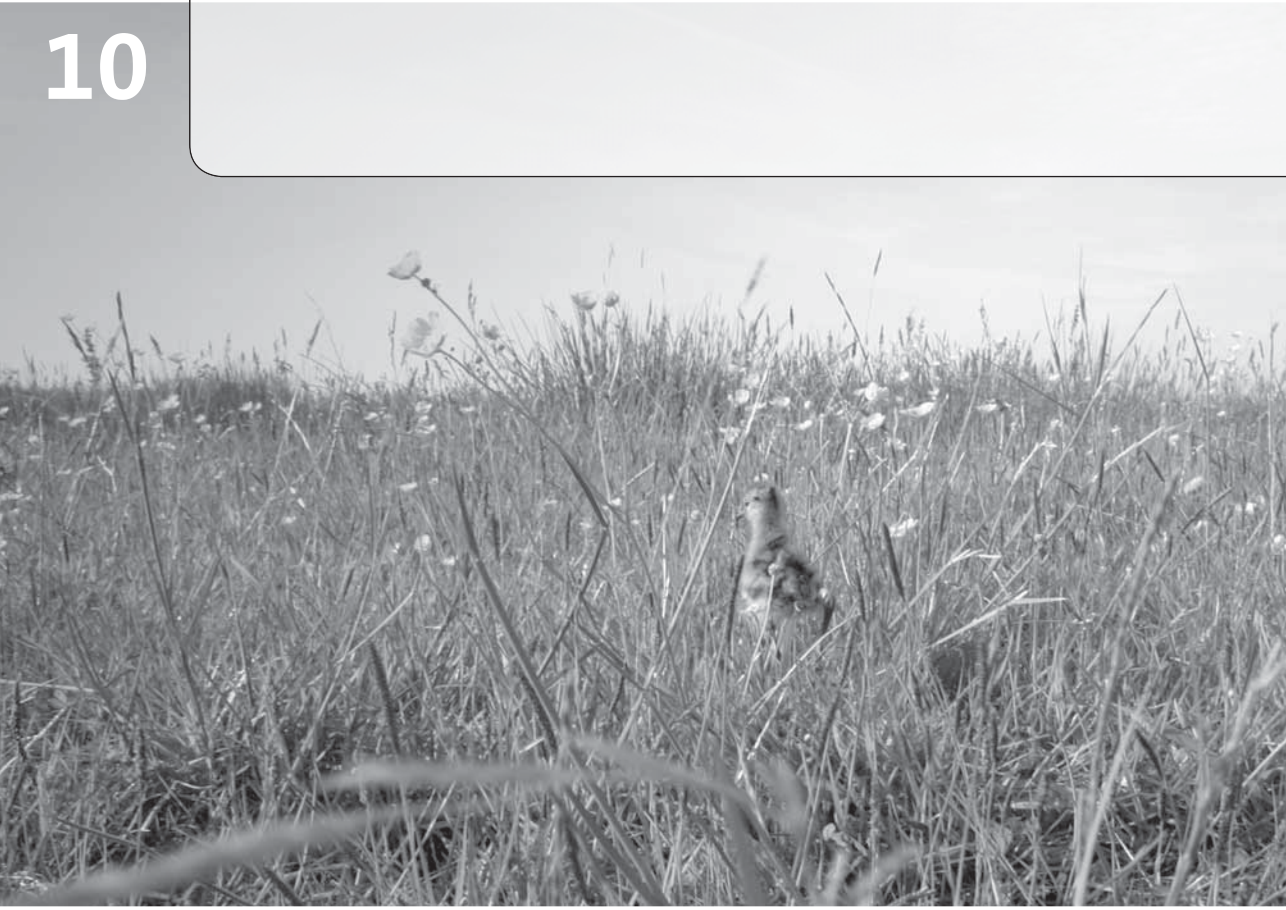
- Tjørve K.M., H. Schekkerman, I. Tulp, L.G. Underhill, J.J. de Leeuw & G.H. Visser 2007a. Growth and energetics of a small shorebird species in a cold environment: the Little Stint *Calidris minuta* on the Taimyr Peninsula, Siberia. Journal of Avian Biology in press.
- Tjørve K.M.C., L.G. Underhill & G.H. Visser 2007b. Pre-fledging energy requirements of the nocturnally fed semi-precocial chicks of the Spotted Thick-knee (*Burhinus capensis*). Emu 107: 143-150.
- Tjørve K.M.C., L.G. Underhill & G.H. Visser 2007c. Energetics of growth in semi-precocial shorebird chicks in a warm environment: the African Black Oystercatcher, *Haematopus moquini*. Zoology 110: 176-188.
- Tjørve K.M.C., L.G. Underhill & G.H. Visser 2008. The energetic implications of precocial development of three shorebird species breeding in a warm environment. Ibis 150: 125-138.
- Troy D. 1996. Population dynamics of breeding shorebirds in Arctic Alaska. International Wader Studies 8: 15-27.
- Tulp I. & H. Schekkerman 2007. Correlates of growth rate in arctic shorebird chicks: daily weather and food abundance. In I. Tulp (2007). The arctic pulse: 169-187. PhD Thesis, University of Groningen.
- Tulp I., H. Schekkerman, B. L.W., J. Jukema, G.H. Visser & Piersma 2007. Incubation and chick-rearing in high arctic breeding shorebirds: what is the most demanding phase? In I. Tulp. The arctic pulse: 121-140. PhD. Thesis, University of Groningen.
- Tulp I. & H. Schekkerman 2008. Weather- and season-related variation in the abundance of tundra arthropods: hindcasting the effect of climate change on prey availability for arctic birds. Arctic 61: 48-60.
- Vedder O., A.L. Dekker, G.H. Visser & C. Dijkstra 2005. Sex-specific energy requirements in nestlings of an extremely sexually size dimorphic bird, the European sparrowhawk (Accipiter nisus). Behavioral Ecology and Sociobiology 58: 429-436.
- Verhulst J., D. Kleijn & F. Berendse 2007. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. Journal of Applied Ecology 44: 70-80.
- Visser G.H. 1991. Development of metabolism and temperature regulation in precocial birds, University of Utrecht, Utrecht.
- Weathers W.W., W.D. Koenig & M.T. Stanback 1990. Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. Condor 92: 341-359.
- Weathers, W.W. & K.A. Sullivan 1991. Growth and energetics of nestling Yellow-eyed Juncos. Condor 93: 138-146.
- Weathers W.W. 1992. Scaling nestling energy-requirements. Ibis 134: 142-153.
- Weathers W.W. & K.A. Sullivan 1993. Seasonal patterns of time and energy allocation by birds. Physiological Zoology 66: 511-536.
- Weathers W.W., C.L. Davidson & M.L. Morton 2003. Energetics of altricial nestlings in cold climates: insights from the Mountain White-crowned Sparrow. Condor 105: 707-718.
- Willems F., C. van Turnhout, H. van Kleef & R. Felix 2002. Breeding birds of Medusa Bay, Taimyr, Russia. WIWO-report 77, WIWO, Zeist.
- Willems F., A. Breeuwer, R. Foppen, W. Teunissen, H. Schekkerman, P. Goedhart, D. Kleijn & F. Berendse 2004. Evaluatie agrarisch natuurbeheer: effecten op weidevogeldichtheden. SOVON-onderzoeksrapport 2004/02, SOVON /WUR /Alterra, Beek-Ubbergen.

- Williams J.B. & A. Prints 1986. Energetics of growth in nestling Savannah Sparrows - a comparison of doubly labeled water and laboratory estimates. Condor 88: 74-83.
- Williams J.B. 2001. Energy expenditure and water flux of free-living Dune Larks in the Namib: a test of the reallocation hypothesis on a desert bird. Functional Ecology 15: 175-185.
- Wretenberg J., A. Lindstrom, S. Svensson & T. Pärt 2007. Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. Journal of Applied Ecology 44: 933-941.
- Wymenga E. & R. Alma 1998. Onderzoek naar de achteruitgang van weidevogels in het natuurreservaat de Gouden Bodem. A&W-rapport 170, Altenburg & Wymenga ecologisch onderzoek, Veenwouden.

Nederlandse samenvatting

Nestvliederperikelen: steltloperkuikens in de ban van klimaat, landbouw en predatie

10



Nestvlieders en nestblijvers

Wanneer jonge grootpoothoenders uit hun ei kruipen dat begraven ligt in een rottende berg plantenmateriaal of in een warme zandbodem, zijn ze voorzien van een goed pak veren en in staat zich naar boven te graven, weg te wandelen, warm te blijven en zelf voedsel te vinden. Ze kunnen zelfs binnen een dag vliegend aan een predator ontsnappen. In groot contrast daarmee komen de kuikens van de meeste zangvogels blind, nagenoeg onbevederd en met weinig ontwikkelde spieren uit het ei. Ze zijn niet in staat tot veel meer dan hun kop oprichten en bedelen wanneer ze iets (een ouder?) het nest horen naderen, aangeboden voedsel inslikken, en verteren. Om warm te blijven en voor hun veiligheid en voedselvoorziening zijn ze geheel aangewezen op hun ouders gedurende een langere periode waarin ze in het nest verblijven, en vaak nog enige tijd daarna. Veel andere vogelgroepen nemen in deze opzichten een tussenpositie in, zodat een continuüm ontstaat van een geringe naar een grote mate van ontwikkeling en zelfstandigheid bij de geboorte. In het Engels worden de uiteinden van dit spectrum aangeduid met de termen *precocial* en *altricial*. In het Nederlands spreken we van 'nestvlieders' en 'nestblijvers', maar dat beschrijft maar één aspect van de variatie, die ook de bevedering, ontwikkeling van spier- en zenuwstelsel, warmtehuishouding en de relatie tussen ouder en kuiken omvat. Op grond van dit soort kenmerken is het spectrum ingedeeld in verschillende groepen (Starck & Ricklefs 1998; fig. 1.1).

De vraag ligt voor de hand welke factoren geleid hebben tot het ontstaan van deze verschillende ontwikkelingswijzen. We weten eigenlijk niet goed of de historische 'oervogel' meer aan de *altricial* dan aan de (waarschijnlijker) *precocial* kant van het spectrum zat. Wel is duidelijk dat het onderscheid al heel vroeg in de evolutionaire geschiedenis van de vogels tot stand is gekomen. Vogelsoorten die behoren tot dezelfde orde, en zelfs tot dezelfde familie, vertonen bijna altijd dezelfde ontwikkelingswijze. Kennelijk is dit een 'evolutionair conservatieve' eigenschap die niet gemakkelijk meer verandert onder invloed van omgevingsfactoren. Omgekeerd kunnen die omgevingsfactoren echter wel degelijk het voortbestaan en het ecologische succes van verschillende vogelgroepen beïnvloeden, bijvoorbeeld via beperkingen in de mogelijkheden om bepaalde habitats of voedselbronnen te benutten. Het is daarom interessant om de ecologische gevolgen van verschillende ontwikkelingswijzen te bestuderen.

Hoewel het *altricial-precocial* spectrum een geleidelijke schaal is, lijken sommige overgangen van fundamenteler betekenis te zijn dan andere. In morfologisch opzicht liggen de grootste verschillen tussen 'echte' *altricials* en alle overige groepen. Meer gedragsmatig heeft het onderscheid tussen nestblijvers en nestvlieders (die het nest verlaten, zich kunnen verstoppen bij gevaar, en soms zelfs de ouders volgen naar het foerageergebied) grote gevolgen voor veiligheid en de economie van de voedselvoorziening. Met name op dat laatste punt is ook belangrijk of de jongen door hun ouders worden gevoerd of vanaf het begin hun eigen voedsel vergaren. De 'last' van het foerageren verschuift daarbij van de ouders naar de kuikens. Die moeten daarvoor hun nest uit en actief zijn in weer en wind, en dat zal hun energieverbruik vergroten in vergelijking met nestblijvers. We weten echter nog maar weinig van de energetische gevolgen van verschillende ontwikkelingswijzen voor opgroeiende vogels. Dat komt onder andere doordat het tot vrij recent moeilijk was om energieuitgaven te meten bij kuikens die zich vrijelijk verplaatsen in het veld. Juist bij zelf foeragerende kuikens kunnen echter in het laboratorium, waar de temperatuur vaak aangenaam is en voedsel zonder moeite beschikbaar, de energieuitgaven gemakkelijk worden onderschat.

Steltlopers zijn een goed voorbeeld van een vogelgroep met zelf foeragerende nestvliederkuikens. De groep omvat een aantal families (o.a. strandlopers en snippen, plevieren, scholeksters, kluten, renvogels en grielen) in de orde van de Charadriiformes, waartoe onder meer ook de meeuwen, sterns en alkachtigen behoren. Deze vogelorde is uitzonderlijk omdat er tussen en zelfs binnen families relatief veel variatie bestaat in ontwikkelingswijze van de jongen. Bij de twee grootste families, de plevieren (Charadriidae) en strandlopers, ruiters en snippen (Scolopacidae) foerageren de jongen echter vanaf de eerste dag voor zichzelf, behalve bij de snippen die korter of langer door hun ouders worden gevoerd. In vergelijking met andere vogels met zelf foeragerende kuikens zoals eenden, ganzen en hoenderachtigen zijn jonge steltlopers vrij slecht in staat zelf hun lichaamstemperatuur op peil te houden. Je zou daarom denken dat steltloperkuikens het beste opgroeien in warmere klimaten, maar opvallend genoeg vinden we de grootste soortenrijkdom in deze groep juist op hogere breedtegraden, onder meer in de arctische toendra's. Dat roept de vraag op hoe de kuikens de hindernissen overwinnen waarvoor het arctische klimaat hen stelt, en wat de toendra tot zo'n favoriete steltloperbroedplek maakt.

Steltlopers als weidevogels

Op onze gematigde breedten broedden van oudsher ook veel steltlopers, zowel langs de kusten als in moerassen, venen en natte graslanden in het binnenland. Toen de mens aan het einde van de Middeleeuwen veel van deze gebieden ging ontginnen en omzette in vochtige graslanden vestigde zich hier een gemeenschap van 'weidevogels'. Naast steltlopers (Watersnip, Kemphaan, Tureluur, Kievit, Grutto, en later ook Wulp en Scholekster) maken ook enkele eenden (Wilde Eend, Slobeend en Zomertaling), en zangvogels (Graspieper, Gele Kwikstaart, Veldleeuwerik, Paapje) daarvan deel uit. Vanaf de tweede helft van de 19^{e} eeuw begon het landbouwkundig gebruik van de Nederlandse graslanden eerst langzaam maar daarna steeds sneller te intensiveren. Belangrijke aspecten daarvan waren een betere ontwatering en een sterke toename in mestgift en veedichtheid. Vooral tussen de tweede wereldoorlog en de jaren '80 van de vorige eeuw is het heel snel gegaan. Hoewel aan de toename van veedichtheid en mestgiften sinds de invoering van Europese mestwetgeving een einde is gekomen, gaan andere aspecten van intensivering, zoals ontwatering en graslandvernieuwing, nog steeds door.

Aanvankelijk hebben weidevogels geprofiteerd van de intensivering, die heeft geleid tot een toename van ondergrondse (regenwormen)fauna. Op een bepaald moment echter gingen andere aspecten van het intensieve landgebruik, met name de steeds vroegere graas- en maaidatums en hoge veedichtheden, het broedsucces van de vogels negatief beïnvloeden. Toen dit het positieve effect van een groter voedselaanbod ging overheersen werden de aantalstoenamen omgebogen in afnamen – eerst bij de kleinere steltlopers en vanaf ongeveer 1960 ook bij de Grutto, gevolgd door de andere grote soorten (fig. 1.2).

De kuikens van de Nederlandse weidesteltlopers zijn, met uitzondering van Scholeksters die door hun ouders met bodemfauna worden gevoerd, zelf foeragerende nestvlieders die insecten, spinnen en andere ongewervelden uit de graslandvegetatie (Grutto, Tureluur, Wulp, de laatste ook wel bodemfauna) of van het bodemoppervlak (Kievit) pikken. Uit eerdere studies blijkt dat de gemiddelde grootte van deze ongewervelden afneemt naarmate de mestgift in graslanden toeneemt. Vermoedelijk hebben bij een intensiever agrarisch graslandgebruik vooral grotere insecten moeite om hun levencyclus te volbrengen. Voor een foeragerende vogel betekent een kleinere gemiddelde grootte van prooien dat hij er meer moet eten om aan zijn dagelijkse voedselbehoefte te voldoen, en dat wordt nog versterkt doordat het 'verwerken' van kleine prooien per eenheid energie die het oplevert meer tijd kost. Het is dus goed mogelijk dat de overstap van meer natuurlijke habitats naar agrarisch grasland en de daarop volgende landbouwintensivering het ondergrondse voedselaanbod voor de volwassen weidevogels weliswaar heeft verbeterd, maar tegelijkertijd het bovengrondse aanbod voor de kuikens verslechterd.

Uiteraard is naast de grootte van insecten ook hun talrijkheid van belang, en ook daarop kan het agrarisch gebruik invloed hebben. Vroeger en vaker maaien is een belangrijk aspect van intensieve veehouderij. Weidevogelkuikens, en dan vooral soorten die hun voedsel vooral uit de vegetatie halen zoals Grutto's, zouden daardoor kunnen worden beperkt in hun foerageermogelijkheden. Daarnaast biedt hoog gras dekking tegen predatoren. Kuikens zijn een lekker hapje voor veel verschillende roofdieren. Lange tijd was ons open weidelandschap niet zo geschikt voor een aantal van deze soorten, die bovendien ook nog onder de duim werden gehouden door jarenlange vervolging of vergiftigingsproblemen veroorzaakt door het gebruik van bestrijdingsmiddelen in de landbouw. In de tweede helft van de vorige eeuw hebben predatoren zoals Vos, Buizerd en Havik het weidelandschap ge(re)koloniseerd doordat deze problemen wegvielen en de mens het gebied voor hen ontsloot door de aanleg van wegen, bruggen, houtsingels en bosjes. De predatiedruk op eieren en jongen van weidevogels is daardoor waarschijnlijk toegenomen.

In de afgelopen decennia zijn in Nederland tal van maatregelen ingezet om te proberen de achteruitgang van weidevogels tot staan te brengen. De belangrijkste daarvan zijn reservaten en beheersovereenkomsten met boeren. Tot dusverre hebben deze de afname van weidevogels echter niet kunnen ombuigen. Kennelijk werken ze nog onvoldoende of worden ze niet grootschalig genoeg toegepast om effectief te zijn. Recent zijn daarom initiatieven ontwikkeld voor intensievere vormen van agrarisch natuurbeheer, die beogen nauwer aan te sluiten bij de behoeften van weidevogels, en dan vooral hun kuikens. Veel maatregelen zijn gericht op de Grutto, omdat Nederland voor deze soort een van de belangrijkste broedgebieden vormt.

In dit proefschrift beschrijf ik een aantal aspecten van de energiebalans en het foerageergedrag van opgroeiende gruttokuikens, en ga na hoe de beschikbaarheid van hun voedsel wordt beïnvloed door het agrarisch graslandgebruik en door de weersomstandigheden. Vervolgens bestudeer ik hoe dit doorwerkt op de overleving van kuikens die met behulp van kleine radiozenders zijn gevolgd. Op die manier onderzochten we ook de effectiviteit van een nieuwe vorm van agrarisch natuurbeheer voor Grutto's. In sommige hoofdstukken wordt ook de Kievit in het verhaal betrokken, als verwante soort die echter wel ecologische verschillen vertoont met de Grutto. Daarnaast maak ik een uitstap naar de arctische broedgebieden van steltlopers om na te gaan welke invloed de hier heersende omstandigheden hebben op de energiebalans en het opgroeisucces van kuikens.

De energetische gevolgen van een zelfstandige jeugd

Hoofdstuk 2 beschrijft de energiebalans van Grutto- en Kievitkuikens, en vergelijkt deze met gepubliceerde metingen aan andere vogelsoorten. We bepaalden de energieuitgaven van kuikens in het veld met behulp van de 'zwaar water methode'. Deze maakt gebruik van de verschillende verdwijningssnelheden van door hun grotere atoomgewicht 'gemerkte' stabiele isotopen van waterstof en zuurstof bij de natuurlijke verbrandingsprocessen in het lichaam. Door een kleine hoeveelheid water verrijkt met deze isotopen in het kuiken in te spuiten, kort daarna en opnieuw een dag later een klein bloedmonster te verzamelen, en daarin de concentratie van 'zware' waterstof- en zuurstofatomen te bepalen, is de productie van koolzuurgas te meten die een directe afspiegeling is van het energieverbruik. Omdat gruttofamilies zich in een dag over flinke afstanden kunnen verplaatsen werden de meeste metingen verricht aan kuikens die opgroeiden in *enclosures* waar zij zelf niet maar hun ouders wel uit konden, maar waarin zij verder geheel zelfstandig naar voedsel zochten in het grasland. Bij de zich minder verplaatsende Kieviten werden de metingen gedaan aan vrij levende kuikens. We combineerden de veldwaarnemingen met metingen van de energieuitgaven in gevangenschap. Daarnaast bepaalden we de lichaamssamenstelling van vogels die op verschillende leeftijden waren gestorven om te achterhalen hoeveel energie er gaat zitten in de aanleg van weefsels tijdens de groei. Zo konden we het energiebudget verdelen in bestedingen aan rustmetabolisme, aanleg van weefsels, het op peil houden van de lichaamstemperatuur (thermoregulatie) en activiteit (zoals foerageren).

Bij beide soorten nam het energieverbruik van de kuikens ongeveer evenredig toe met het lichaamsgewicht (fig. 2.1). De totale energieuitgaven tussen geboorte en het uitvliegen waren 39% (Grutto) en 29% (Kievit) groter dan verwacht op grond van een relatie tussen het energieverbruik en het gewicht en de leeftijd bij uitvliegen gevonden door Weathers (1992) bij 30 andere vogelsoorten, waarvan er 28 door hun ouders werden gevoerd. Het ligt voor de hand dat dit komt doordat de zelf foeragerende weidevogelkuikens door hun actieve levenswijze meer energie uitgeven aan activiteit en thermoregulatie dan kuikens die in een beschut nest liggen. Inderdaad bleken deze twee kostenposten bij de weidevogels ruim twee maal zo'n groot deel te vormen van het energiebudget dan bij zeven door hun ouders gevoerde vogelsoorten (fig. 2.5).

Doordat we de energieuitgaven zowel in het veld als aan kuikens in gevangenschap hadden gemeten, konden we ook nagaan hoe groot de onderschatting is die in het laboratorium optreedt doordat de temperatuur er gunstiger is en voedsel zonder moeite beschikbaar. In gevangenschap gaven de kuikens 26-31% minder energie uit dan bij de zelfde groeisnelheid in het veld; bij metingen van het zuurstofverbruik in kleine metabole kamers, zou het verschil zelfs kunnen oplopen tot 50-53%. Het is dus belangrijk om energieverbruik te meten onder veldomstandigheden.

Dat hebben we ook gedaan bij kuikens van de Kanoet en de Kleine Strandloper die opgroeiden in de toendra van noordelijk Siberië (hoofdstuk 3, Tjørve *et al.* 2007). Bij die soorten lag het energieverbruik zelfs 89% en 110% boven de voorspelling van Weathers, een gevolg van de combinatie van hun actieve levensstijl en het koude arctische klimaat. In hoofdstuk 9 heb ik alle beschikbare schattingen van het energieverbruik van opgroeiende vogeljongen, gemeten in het veld met de zwaar water methode, samen geanalyseerd. Daaruit blijkt dat de energiebehoefte behalve van de grootte en de groeisnelheid van het kuiken ook sterk afhankelijk is van de temperatuur. Rekening houdend met al die factoren is het verbruik van zelf foeragerende nestvliederkuikens zo'n 40% groter dan dat van door hun ouders gevoerde nestblijvers (fig. 9.1). De energiebehoefte van nestvlieders die door hun ouders worden gevoerd ligt daar tussen in.

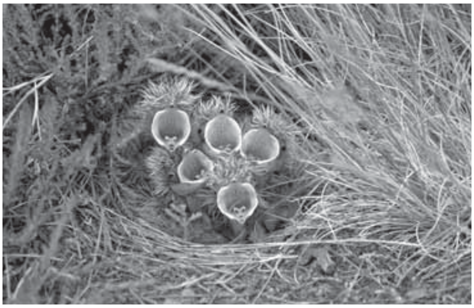
Zelf foeragerende nestvlieders hebben dus om op te groeien meer voedsel nodig dan door hun ouders gevoerde vogeljongen. Daarnaast valt te verwachten dat ze gevoeliger zijn voor kortdurende stagnaties in het voedselaanbod. Omdat steltloperkuikens zo'n groot deel van de binnenkomende energie weer uitgeven aan activiteit en thermoregulatie is het deel dat daadwerkelijk aan groei wordt besteed kleiner dan bij nestblijvers (23-27% tegen 24-52%). Dat betekent dat het relatief inefficiënte groeiers zijn, en er al bij een vrij geringe afname van de inkomsten (voedselgebrek) of verhoging van de uitgaven (zoals bij koud weer) geen energie meer overblijft voor groei. En terwijl nestblijverkuikens bij schaarste kunnen bezuinigen op activiteit, en (eventueel bebroed door een ouder) afwachten tot voer wordt aangebracht leidt zo'n bezuiniging bij een zelf foeragerende nestvlieder onmiddellijk tot een verdere reductie van de voedselopname. Bovendien is het denkbaar dat kuikens die eenmaal achterop zijn geraakt in groei daardoor minder goed functioneren, en zo in een negatieve spiraal terecht komen. Bij nestblijvers is dat gevaar minder groot omdat de foerageercapaciteit van de ouders niet wordt bepaald door de conditie van de jongen.

In hoofdstuk 5 bestuderen we de ontwikkeling van foerageergedrag en voedselopname van gruttokuikens die opgroeiden in *enclosures* waar we hun tijdsbesteding en foerageersucces konden waarnemen. Ook bepaalden we van deze kuikens elke paar dagen het gewicht. De dagelijkse voedselopname van gruttokuikens is het product van de tijd die ze aan foerageren besteden en de opnamesnelheid die ze tijdens het foerageren behalen. De foerageertijd wordt begrensd door de daglichtperiode en de noodzaak af en toe opgewarmd te worden door een ouder. Tot ze ruim een week oud zijn, zijn de kuikens onder koude omstandigheden nog niet in staat om hun lichaamstemperatuur op peil te houden. Kuikens die achterbleven in groei werden bij dezelfde leeftijd en weersomstandigheden meer bebroed dan kuikens in een normale conditie (fig. 5.2) en hielden dus minder tijd over om te foerageren. Nu geven lichtere kuikens ook minder energie uit, dus of dit echt kan leiden tot een neerwaartse spiraal is nog de vraag. We namen in ieder geval niet waar dat zulke kuikens ook minder succesvol foerageerden; ze vingen per minuut even veel insecten als kuikens in goede conditie. Toch blijft het gevaarlijk om achterop te raken: bij gruttokuikens die met een kleine radiozender waren uitgerust bleek dat de kans om te 'verdwijnen' (vermoedelijk vooral door predatie) ook al toenam voordat de conditie zo slecht geworden was dat het kuiken van uitputting stierf.

Wanneer heeft zelf foerageren voordelen?

Zelf-foeragerende kuikens lijken dus in vergelijking met gevoerde vogeljongen afhankelijker van een rijk en betrouwbaar voedselaanbod. Daar komt bij dat nog onvolledig ontwikkelde kuikens de kracht en de behendigheid missen om bepaalde voedselbronnen te exploiteren die volwassen vogels wel kunnen benutten (en aan hun jongen voeren). Kuikens doden geen andere vogels of kleine zoogdieren, duiken niet naar vis, en bemachtigen geen ingegraven schelpdieren, allemaal voedseltypen die rijk zijn aan energie en voedingsstoffen. Zelfs hele biotopen zoals open water en boomkruinen kunnen door hen niet worden benut als foerageergebied.

Toch heeft zelf foerageren niet alleen maar nadelen. Het maakt het voor vogels gemakkelijker om kleine of energetisch laagwaardige voedselbronnen te exploiteren, zoals kleine insecten en gebladerte. Als zulk voedsel door de ouders naar de jongen gebracht moet worden levert dat niet alleen voor de ouders (vlieg)kosten op maar ook voor de kuikens, doordat de tijd die aan het transport verloren gaat de profijtelijkheid (energieopbrengst per seconde verwerkingstijd) van de prooi verlaagt. Als kuikens zelf foerageren is transport niet nodig en kunnen kleinere prooien of voedsel met een geringe energie-inhoud toch nog profijtelijk zijn. Vogels kunnen dit transportprobleem gedeeltelijk omzeilen door hun jongen mee te nemen naar het voedselgebied en daar te voeren (zoals Scholeksters doen) of door meerdere prooien in één keer te vervoeren, maar beide opties hebben hun beperkingen. Daar komt bij dat bij nestblijvers doorgaans één of twee oudervogels alle voedsel voor het gehele broedsel bijeen moeten brengen, terwijl bij zelf foeragerende nestvlieders meer snavels en ogen het werk kunnen doen. Oudervogels die hun jongen voeren zullen daardoor bij een afnemende gemiddelde grootte of energie-inhoud van prooien eerder problemen ondervinden om hun jongen binnen de beperkte tijd van een dag van voldoende voedsel te voor-



zien dan kuikens die voor zichzelf zorgen (fig. 9.2). Het is opvallend dat de meeste zelf foeragerende nestvlieders als jong kleine insecten, gebladerte en ander plantaardig voedsel eten, zelfs (middel)grote soorten zoals hoender- en struisvogelachtigen, eenden, ganzen en zwanen. Nestblijvers die hun jongen voeren met kleine insecten zijn doorgaans niet veel groter dan een lijster, en er is maar één nestblijver die zijn jongen voedt met (voorverteerd) gebladerte: de Hoatzin uit Zuid-Amerika.

Het ligt voor de hand dat de afwezigheid van de noodzaak om inspannende foerageertochten voor de jongen uit te voeren de oudervogels veel energie bespaart. Daardoor zouden ze in staat kunnen zijn om meer jongen in één keer groot te brengen, of beter te overleven en vaker te broeden. Het wegvallen van één ouder hoeft ook niet zo snel fataal te zijn voor de jongen, en dat maakt het eerder lonend om te proberen via polygamie meer nakomelingen op de wereld te zetten. Bij vogelsoorten met (zelf foeragerende) nestvliederkuikens komen broedzorg door één ouder en polygamie inderdaad vaker voor dan bij nestblijvers.

Het nestvliederschap kan ook gevolgen hebben voor predatierisico, maar dat kan twee kanten op werken (tabel 9.3). Enerzijds neemt dit risico af wanneer het broedsel het nest kan verlaten en uit de buurt van een predator weglopen, de kuikens zich afzonderlijk verstoppen zodat ze niet allemaal tegelijk gevonden worden, en de ouders geen door herhaling opvallende voedselvluchten uitvoeren. Daar staat tegenover dat de noodzaak om actief te foerageren de kuikens ook zichtbaar kan maken voor predatoren, en dat deze ontwikkelingswijze samengaat met een langzamere groei van embryo's en kuikens die leidt tot een langduriger blootstelling. Het netto resultaat kan daardoor variëren met de vogelsoort, soort predator, en de habitat.

Groeien in de toendra

Veel soorten steltlopers broeden in de arctische toendra, waar kuikens bij de lage temperaturen veel energie nodig hebben om op te groeien. Bovendien valt te verwachten dat ze er vaak opgewarmd moeten worden en zo kostbare foerageertijd verliezen. Toch groeien arctische steltloperkuikens juist sneller dan familiegenoten op lagere breedten. Kennelijk zijn er factoren die de nadelen van het koude klimaat compenseren. Om erachter te komen welke dat zijn bestudeerden we de energieuitgaven, activiteit, variatie in groeisnelheid en het voedselaanbod voor jonge Kanoeten op het Taimyr-schiereiland in Noord-Siberië, en vergeleken dat met die van kuikens in Hollandse graslanden (hoofdstuk 3). Kanoetenfamilies zijn goed te benaderen en laten zich vanaf korte afstand observeren. Ze dag na dag terugvinden in de uitgestrekte toendra is lastiger, maar werd vergemakkelijkt doordat we twee van de begeleidende vaders van een zender hadden voorzien.

Jonge Kanoeten werden een stuk minder vaak bebroed dan kuikens van Grutto, Tureluur en Kievit bij dezelfde temperaturen in Nederland (fig. 3.4). Of ze dat klaarspelen door harder te 'stoken' of door een beter isolerend verenkleed weten we niet, maar het helpt hen enorm om de beperking in foerageertijd die de kou hen oplegt te minimaliseren, vooral in de eerste levensdagen. Een tweede factor die daarbij helpt is het feit dat het in de poolzomer 24 uur per dag licht is. Toch profiteerden de kuikens daar niet volledig van: in de 'nachtelijke' uren werden ze langduriger bebroed dan je op grond van de temperatuur zou verwachten. Misschien is het insectenaanbod dan gering, maar het is ook mogelijk dat de kuikens een dagelijkse portie slaap nodig hebben die ze niet kunnen verwerken in de reguliere broedbeurten. De snelle groei van de kuikens helpt zelf ook mee, doordat met toenemende grootte de verhouding tussen oppervlak (dat warmte verliest) en inhoud (die warmte genereert) van een lichaam gunstiger wordt. Uiteindelijk hebben Kanoetenkuikens door deze drie factoren bij 3°C in de toendra ongeveer net zo veel tijd om te foerageren als een Tureluurkuiken bij 15°C. Omdat Kanoetenkuikens meer energie uitgeven dan de ongeveer even grote Tureluurs moeten ze echter in die zelfde tijd wel meer voedsel opnemen (fig. 3.6, 3.7). Hoewel de midzomerpiek in het aanbod van insecten in de toendra welhaast legendarisch is, vonden we er in een bemonstering met potvallen gemiddeld geen grotere aantallen ongewervelden dan in een Nederlands grasland. Het lijkt erop dat niet zo zeer de aantallen maar vooral een betere vangbaarheid van insecten in de ijle vegetatie de toendra tot een profijtelijker foerageergebied maakt.

De insecten die rondscharrelen op en net boven het bodemoppervlak zijn overigens wel een factor die kan helpen verklaren waarom steltlopers een groot deel uitmaken van de vogelbevolking van de toendra. Er is hier maar weinig groter dierlijk voedsel te eten, tenzij je zo sterk bent dat je de in sommige jaren talrijke lemmingen kunt bemachtigen. Zoals we hebben gezien zijn zelf foeragerende nestvliederkuikens goed in staat zulke kleine prooien te exploiteren. Terwijl in hoogarctische toendra steltlopers voorkomen tot een grootte van 230 gram (Zilverplevier) weegt de grootste vogelsoort die er insecten naar zijn jongen brengt (Strandleeuwerik) niet meer dan 32 g (fig. 9.4).

De beschikbaarheid van insecten kan op de toendra echter van dag tot dag sterk variëren. Hun activiteit is afhankelijk van de temperatuur, zo bleek ook uit onze bemonstering. De groei van Kanoetenkuikens werd hierdoor sterk beïnvloed: wanneer de insectenvangsten daalden tot minder dan *c.* 5 mg drooggewicht per potval per dag liep de groeisnelheid van de kuikens snel terug, en op slechte dagen vielen ze zelfs af (fig. 3.3). Hoge energieuitgaven en een korte foerageertijd door extra bebroeding op koude dagen dragen daaraan ook bij, maar de groeisnelheid was het sterkst gecorreleerd met de insectenactiviteit. Vanaf het einde van juli loopt deze vaak terug, ook op warme dagen; de ‘zomerpiek’ is dan voorbij. Laat geboren kuikens hadden daardoor gemiddeld minder te eten dan vroeg geboren jongen. In ons studiejaar hadden de Kanoeten echter niet veel eerder kunnen beginnen met broeden dan ze deden, omdat de toendra nog niet eerder sneeuwvrij was. De korte duur van gunstige omstandigheden om te broeden is waarschijnlijk één van de factoren die selecteert voor een snelle groei bij arctische kuikens.

Een effect op groeisnelheid is nog geen effect op overleving, maar dat laatste is bij nestvliederkuikens niet gemakkelijk in het veld te meten, juist doordat ze mobiel zijn en zich goed kunnen verstoppen. Gelukkig concentreren veel arctische steltlopers zich 's winters in kustgebieden op lagere breedten, waar we het succes van het voorafgaande broedseizoen kunnen afmeten aan het aandeel jonge vogels in de populatie. In hoofdstuk 4 analyseren we zulke gegevens voor de Krombekstrandloper. Veldwerk in het broedgebied in Taimyr liet zien dat ook bij deze soort het insectenaanbod en de groeisnelheid van kuikens beïnvloed worden door de weersomstandigheden. Daarnaast beschikten we over een reeks van 18 jaar vangstgegevens van 'overwinterende' Krombekstrandlopers uit Zuid-Afrika, en gegevens over de omstandigheden in Taimyr in die jaren. Het aandeel juveniele krombekken in de ringvangsten vertoonde grote jaarlijkse variatie, die nauw samenhing met de aantallen lemmingen op de toendra in de voorafgaande zomer. In lemmingrijke jaren hebben predatoren zoals Poolvossen en Middelste Jagers zat te eten en talen ze niet naar steltlopereitjes en -kuikens. Als er weinig lemmingen zijn kan de predatiedruk op vogels echter zeer hoog zijn. Als we hiermee rekening hielden was er echter ook een duidelijk effect zichtbaar van de weersomstandigheden in Taimyr precies in de periode waarin de krombekkuikens uit het ei komen – en niet in andere delen van de zomer. De grootste aantallen jonge vogels kwamen naar Zuid-Afrika in jaren met een matige of hoge lemmingdichtheid waarin de gemiddelde temperatuur op Taimyr rond midden juli boven de 7-10°C uitkwam (fig. 4.6). Dit laat zien dat weersomstandigheden en voedselaanbod tijdens de opgroeiperiode inderdaad grote invloed hebben op de overleving van steltloperkuikens.

Hoe gruttokuikens hun kostje bijeen scharrelen

De meeste steltloperkuikens foerageren dus vanaf de eerste dag voor zichzelf, maar hoe gaat dat eigenlijk in zijn werk? Hoeveel tijd zijn ze kwijt aan foerageren, en zit daar ruimte in om tegenvallende foerageeropbrengsten op te vangen? Hoe gevoelig is foerageersucces voor weersomstandigheden en voedselaanbod? En hoe verandert het foerageergedrag met de leeftijd, naarmate met de kuikens zelf ook hun voedselbehoefte groeit? In vier seizoenen hebben we intensieve waarnemingen verricht aan gruttokuikens die opgroeiden in *enclosures* in een als weidevogelreservaat beheerd graslandgebied in de Eempolders bij Baarn. Daarvoor werden 0.2-0.6 ha grote delen van een perceel afgezet met een 50 cm hoog gaashek waar de grutto-ouders wel maar de kuikens niet uit (en in) konden. Zo konden wij vanuit een naast de *enclosure* opgestelde schuilhut de tijdsbesteding van de gruttofamilie en het foerageergedrag van de jongen in detail volgen. Daarbij werd elke minuut genoteerd welke activiteit de kuikens vertoonden: foerageren, bebroed worden door een ouder, rusten, etc. Wanneer de kuikens goed genoeg zichtbaar waren deden we ook waarnemingen aan hun foerageersucces, door het aantal prooien te tellen dat per minuut werd ingeslikt. Verreweg de meeste gegeten insecten waren te klein om te herkennen of hun grootte te schatten, maar de slikbewegingen waren met enige oefening goed herkenbaar. Door onze waarnemingen te combineren met metingen aan het energieverbruik van kuikens (beschreven in hoofdstuk 2) konden we bovendien reconstrueren hoe groot de prooien waren die ze op verschillende leeftijden aten. De energie die een kuiken dagelijks verbruikt of vastlegt in groei moet immers binnenkomen in de vorm van voedsel. Als bekend is hoe lang het kuiken foerageert en hoeveel insecten hij daarbij opneemt valt uit te rekenen hoeveel energie een prooi gemiddeld vertegenwoordigt, en dus hoe groot hij bij benadering is.

Gruttokuikens worden tot een leeftijd van 8-10 dagen geregeld door hun ouders bebroed. Dit neemt af met de leeftijd en met toenemende temperatuur, en gebeurt dus vooral veel in de vroege ochtend en in de avond. ’s Nachts en bij serieuze regenval worden kuikens vrijwel continu bebroed. Van de tijd die niet opgaat aan bebroeding wordt het overgrote deel besteed aan foerageren; bij kuikens ouder dan een week is dat 70-90% van de daglichtperiode. De foerageeractiviteit is het grootst in de morgen en vaak iets kleiner in de (vroege) middag, vooral op warme dagen (fig. 5.1). Door ook stapfrequenties en paslengtes van foeragerende kuikens te meten konden we schatten welke afstanden tijdens het foerageren worden afgelegd. Die lopen op van 3-4 km in de eerste dagen tot 5-12 km per dag voor oudere kuikens. In de 25 dagen totdat kuikens vliegvlug zijn leggen ze ruim 200 km af!

Foeragerende gruttokuikens kuieren door de graslandvegetatie en pikken in het voorbijgaan met een snelle beweging insecten en andere ongewervelden op die ze met het oog ontdekken. Beintema *et al.* (1991) hebben door analyse van kuikenpoep laten zien dat een heel breed spectrum aan ongewervelden gegeten wordt. Wij zagen dat bijna alle prooien uit de vegetatie worden gepikt, en slechts *c.* 1% van of uit het bodemoppervlak. Pas enige tijd nadat ze vliegvlug zijn schakelen kuikens over op het op de tast foerageren op bodemfauna, zoals volwassen grutto’s doen. Het aantal prooien dat per minuut foerageren wordt ingeslikt verdrievoudigt in de eerste levensweek, om daarna te blijven schommelen rond zo’n 10 per minuut (fig. 5.3). Dat zijn 5 000-12 000 insecten per dag. De toename in de eerste week komt tot stand doordat kuikens sneller gaan lopen, en dus per tijdseenheid een groter oppervlak afzoeken. Dit verloopt ongeveer evenredig met de toename van het energieverbruik door de groei, zodat de gemiddelde grootte van de gegeten prooien min of meer constant blijft: 1-1.5 mg drooggewicht, overeenkomend met een gemiddelde lichaamslengte van insecten van 4-5 mm. Na een dag of 10 houdt de prooiopnamesnelheid de groei van het energieverbruik niet langer bij, wat betekent dat de gemiddelde grootte van de gegeten prooien moet toenemen, tot zo’n 3-4.5 mg (6-8 mm). Ongeveer tegelijkertijd neemt ook de loopsnelheid van foeragerende kuikens niet meer toe, en zelfs iets af. Dit wijst er op dat kuikens een andere foerageertactiek gaan gebruiken, en zorgvuldiger gaan zoeken om de grotere ongewervelden in het grasland te vinden (fig. 5.3).

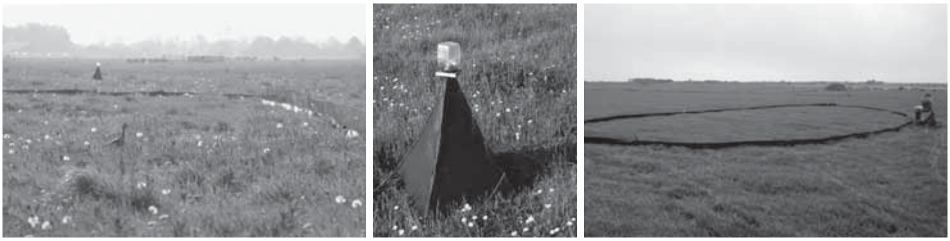
Door bemonsteringen met pyramidevallen (hoofdstuk 6) hebben we ook een goed beeld van de grootteverdeling van de ongewervelden in de graslandvegetatie. Er zijn heel veel kleine insecten en maar weinig grote (fig. 5.5). Kuikens kunnen echter de kleinste insecten, tot 1-3 mm afhankelijk van hun leeftijd, niet goed benutten doordat ze in de tijd die nodig is om deze in te slikken meer energie uitgeven dan de prooi oplevert. Grote insecten zijn veel profijtelijker maar komen in zulke geringe dichtheden voor dat kuikens er lang naar moeten zoeken. Naarmate de kuikens groter groeien wordt dit probleem nijpender. In agrarisch grasland lopen foeragerende gruttokuikens dus tegen de grenzen van een exploiteerbare prooigrootteverdeling aan, en dat zal ze gevoeliger maken voor effecten van weer en landgebruik op het insectenaanbod.

Het foerageersucces van gruttokuikens wordt inderdaad beïnvloed door de weersomstandigheden. Wind heeft het grootste effect en leidt tot een afname van het foerageersucces, vooral bij sterktes boven 3-4 Beaufort. Wellicht zitten er bij stevige wind minder insecten op gemakkelijk zichtbare plekken in de vegetatie of hebben de kuikens in het bewegende gras moeite om ze te ontdekken of te pakken. Ook een toenemende temperatuur lijkt het succes te verlagen, maar dat effect kon niet goed worden onderscheiden van de invloed van tijd van de dag. De opnamesnelheid is het grootst in de vroege morgenuren en neemt vaak opnieuw wat toe tegen de avond. Dat zou zijn te verklaren doordat koude en daardoor 'slome' insecten gemakkelijk zijn te pakken, maar het is ook mogelijk dat kuikens na een nacht vasten door honger meer hun best doen om voedsel te vinden. Ook regen heeft een negatief effect op het foerageersucces, maar dat is vrij beperkt. Bij hevige regen stoppen kuikens echter helemaal met foerageren.

Kuikenvoer en graslandbeheer

De sterke intensivering van het agrarische graslandgebruik heeft onder meer geleid tot sterk toegenomen bemestingsniveaus en tot vroeger en vaker maaien. Dat heeft grote gevolgen voor de vegetatiesamenstelling van graslanden, maar mogelijk ook voor het voorkomen van insecten en andere ongewervelden. Er zijn aanwijzingen dat grotere insecten schaarser worden naarmate grasland intensiever bemest en gebruikt wordt, maar de totale biomassa neemt daarbij lang niet altijd af. Door de grotere productie van plantenmateriaal is er immers in principe meer voedsel beschikbaar voor (plantenetende) insecten. Of dat ook werkelijk benut wordt kan onder meer afhangen van factoren zoals begrazingsdruk en maairegime, die mede bepalen of insecten in het grasland hun levenscyclus kunnen volbrengen.

We hebben onderzocht hoe agrarisch graslandbeheer doorwerkt op het voedselaanbod voor gruttokuikens, door dit te vergelijken tussen graslanden gebruikt voor moderne zuivelproductie (mestgift *c.* 250 kg N/ha/jaar, twee tot drie sneden kuilgras per jaar vanaf begin mei) en beheerd als weidevogelreservaat (*c.* 100 kg N/ha/jaar, één snede per jaar rond 15 juni, gevolgd door extensieve begrazing), en bij twee verschillende slootpeilen. In 1993-1996 bemonsterden we van eind april tot begin juli wekelijks het insectenaanbod op acht percelen met behulp van pyramidevallen (hoofdstuk 6). Voorafgaande aan de eerste maaisnede op de agrarische percelen waren de aantallen ongewervelden iets groter in het reservaatsgrasland, maar verschilde de biomassa niet tussen de typen doordat kevers (relatief groot maar door kuikens waarschijnlijk niet zo veel gegeten) talrijker waren op het boerenland. In de vier tot zes weken tussen



de eerste snede van agrarisch grasland en die in het reservaat waren alle belangrijke groepen insecten en spinnen echter veel algemener in de ongemaaide vegetatie van het reservaat. Juist in deze periode zijn de meeste gruttokuikens aanwezig in de Nederlandse graslanden. Nadat ook in het reservaat was gemaaid verdwenen de verschillen of waren insecten talrijker in het hergroeiende agrarische grasland (fig. 6.2). Hoewel er een tendens was in de richting van meer insecten in de drogere percelen was het effect van waterpeil niet significant. In de praktijk gaat een laag waterpeil echter vaak samen met een vroege maaidatum, waardoor het netto effect van peilverlaging op het voedselaanbod voor kuikens veelal negatief zal zijn.

De gemiddelde grootte van individuele ongewervelden nam af in de loop van het voorjaar en was vroeg in het seizoen groter op agrarische percelen, maar later niet meer. Het lijkt er op dat de in eerdere onderzoeken gevonden afname van de grootte van ongewervelden met toenemende mestgift en gebruiksintensiteit vooral plaatsvindt bij mestgiften lager dan 100 kg N/ha/jaar (fig. 6.5). Dat zou betekenen dat de beperkingen in de grootteverdeling van beschikbare prooien die gruttokuikens ondervinden alleen zijn op te heffen door een sterke beperking van de mestgift, zoals gebeurt bij beheer gericht op botanische natuurwaarden van grasland. Het zou interessant zijn om te onderzoeken hoe de grootteverdeling er uitziet in de natuurlijke graslanden en veengebieden die het oorspronkelijk broedhabitat van Grutto's vormden.

Een geringere dichtheid van insecten in grasland betekent nog niet noodzakelijkerwijs dat gruttokuikens ook een geringer foerageersucces behalen. Daarom hebben we dit geverifieerd in een experiment waarin we kuikens lieten foerageren in kleine *enclosures* op negen gemaaide agrarische percelen en negen ongemaaide reservaatspercelen. Vrij levende gruttofamilies hebben een sterke voorkeur om te verblijven in ongemaaid (reservaats)grasland en trekken daar over aanzienlijke afstanden naar toe, zoals bleek uit systematische waarnemingen aan de verspreiding van nesten en families. Omdat vrij levende families zich niet laten verleiden langdurig te foerageren in recent gemaaid grasland gebruikten we voor dit experiment kuikens die we zelf hadden uitgebroed en opgekweekt. Dat deden we in een grote volière waarin ze werden gevoerd maar ook veel tijd doorbrachten met zelf naar insecten zoeken in het gras. In ongemaaide percelen vonden deze kuikens 31% meer insecten per minuut foerageren dan in gemaaid boerenland. Omdat gruttokuikens gemiddeld maar 26% van hun energie-inkomsten daadwerkelijk aan groei spenderen (hoofdstuk 2) en nauwelijks langer kunnen foerageren dan de 11-14 uur per dag die ze er in het reservaat al aan besteden (hoofdstuk 5) zal zo'n grote afname van het foerageersucces gevolgen hebben voor hun groeisnelheid en overleving. Het uitstellen van de eerste snede is dan ook een belangrijk middel om de opgroeiomstandigheden voor gruttokuikens te verbeteren. Na begin juni heeft uitstel echter niet zo veel zin meer, omdat – ten minste in bemest grasland – dan de vegetatie te dicht wordt en het insectenaanbod afneemt. Ongemaaide percelen worden dan minder aantrekkelijk voor gruttogezinnen.

Een nieuwe beheersvorm voor grutto's

Uitgestelde maaidatums zijn al vanaf het begin onderdeel van de beheersovereenkomsten die de overheid met boeren afsluit om weidevogels te beschermen, maar toch nemen de aantallen vogels nog steeds af. In de afgelopen jaren lieten enkele vergelijkende studies ook zien dat de dichtheden van broedende weidevogels niet hoger waren en/of zich niet gunstiger ontwikkelden op percelen met zulke beheersovereenkomsten dan op gangbaar beheerde percelen. Mede in reactie daarop zijn nieuwe, intensievere vormen van agrarisch natuurbeheer ontwikkeld die beogen beter aan te sluiten op de behoeften van de vogels. Eén hiervan is 'mozaïekbeheer', waarbij groepen boeren hun graslandgebruik op gebiedsniveau (meestal een polder of een deel daarvan) onderling afstemmen om binnen de speelruimte van een agrarische bedrijfsvoering de voortplantingscondities voor Grutto's (en impliciet ook andere weidevogels) te optimaliseren. Basis- principes daarbij zijn het aanbieden van voldoende geschikt grasland dat voedsel en dekking biedt aan gruttokuikens gedurende hun gehele opgroeiperiode, en het realiseren van een mozaïek waarin verschillende graslandtypen op elk moment binnen bereikbare afstand aanwezig zijn. Dit gebeurt door een mix van maatregelen, waaronder maaien met intervallen van een week op aangrenzende percelen (maaitrappen), maaien na 1, 8, 15 of 22 juni, het overlaten van 'vluchtstroken' tijdens het maaien, (voor)beweiding, stalvoerwinning en aanleg van plas-dras, aangevuld met nestbescherming en een aangepaste snelheid bij het maaien. In 2003-2005 is deze beheersvorm in de praktijk getoetst in zes gebieden verspreid in Laag-Nederland.

Hoofdstuk 7 beschrijft onderzoek naar de effectiviteit van het mozaïekbeheer voor Grutto's. We maten het voortplantingssucces en niet aantallen broedvogels zoals in eerdere evaluaties van agrarisch natuurbeheer, omdat de beheersmaatregelen gericht zijn op het verhogen van dit succes, omdat je bij een langlevende vogelsoort als de Grutto eerder effecten zijn te verwachten op de reproductie dan op aantallen, en omdat broedsucces een zuivere maat is voor de bijdrage van het beheer aan de populatie. Dit in tegenstelling tot lokale aantallen die ook beïnvloed worden door immigratie en emigratie. Om succesvol te zijn moet het beheer leiden tot een verhoging van de reproductie, en daarnaast moet deze op zijn minst hoog genoeg zijn om de jaarlijkse sterfte van volgroeide vogels te compenseren zodat de lokale populatie zichzelf in stand houdt. Om dat te onderzoeken bepaalden we het broedsucces in elk van de zes mozaïekgebieden en in zes daarmee gepaarde, nabijgelegen controlegebieden, door gegevens over de uitkomst van een groot deel van de aanwezige nesten te combineren met gegevens over de overleving van een kleinere steekproef van kuikens. Om kuikenoverleving te meten werden ofwel de kuikens zelf, ofwel een van hun ouders voorzien van een zender (zie ook hoofdstuk 8).

Het reproductiesucces van Grutto's was groter in de mozaïekgebieden (gemiddeld 0.28 vliegvlugge jongen per paar) dan in de controlegebieden (0.16), maar dit kwam geheel tot stand door een grotere uitkomstkans van legsels, die op zijn beurt weer een gevolg was van geringere agrarische nestverliezen. De grotere intensiteit van nestbeschermingsactiviteiten in de mozaïekgebieden was hiervan waarschijnlijk een belangrijke oorzaak; predatieverliezen verschilden niet tussen de twee groepen gebieden. Hoewel veel van de onderdelen van het mozaïekbeheer speciaal gericht zijn op kuikens was de kuikenoverleving niet hoger in de mozaïekgebieden. Een van de belangrijkste doelen, het vergroten van het aanbod aan ongemaaid grasland als foerageergebied voor kuikens ten opzichte van gangbaar gebruikt grasland, werd in de praktijk niet bereikt doordat perioden met regen de boeren noopten om het maaien uit te stellen in beide soorten gebieden. Doordat de maaiers een inhaalslag maakten toen het weer opknapte kwam ook het mozaïek minder goed uit de verf. Los van het onderscheid tussen mozaïek- en controlegebieden vertoonde de kuikenoverleving echter wel een positief verband met het aanbod van ongemaaide percelen en ander 'kuikenland' in de kuikenperiode (fig. 7.2). Dit geeft aan dat het basisidee dat later maaien goed is voor kuikens wel opgaat, en suggereert dat in jaren met beter weer in mei een betere kuikenoverleving wel zal bijdragen aan het grotere broedsucces in de mozaïeken. Tegelijkertijd betekent het dat het beheer in natte jaren geen waar voor zijn geld levert, tenzij de voorschriften zo worden aangepast dat het maaien ook na een periode van uitstel nog gespreid wordt in tijd en ruimte.

Hoewel het broedsucces wel groter was in de gebieden met mozaïekbeheer, was het ook daar maar in één gebied meer dan de *c.* 0.6 vliegvlugge jongen per paar die een zichzelf in stand houdende populatie moet produceren. In de controlegebieden werd die waarde nergens gehaald (fig. 7.3). Dat betekent dat ook in de mozaïeken het beheer op de lange termijn niet effectief is, en dus nog verbeterd moet worden.

Doodsoorzaken van kuikens

In het voorgaande zijn een afnemend voedselaanbod voor kuikens onder invloed van bemesting en intensief maaibeheer al genoemd als factoren die het reproductiesucces van weidevogels aantasten. In de afgelopen jaren is daarnaast onder sommige groepen de bezorgdheid toegenomen dat een toenemende predatiedruk op weidevogellegsels en -kuikens de populatieafnames veroorzaakt of het succes van herstelmaatregelen in de weg staat. Over de frequentie van predatie op weidevogelkuikens, en over de doodsoorzaken van kuikens in het algemeen, waren echter nauwelijks systematisch verzamelde gegevens voorhanden.

Hoofdstuk 8 beschrijft resultaten van twee onderzoeksprojecten waarin de lotgevallen van grutto- en kievitkuikens werden gevolgd met behulp van radiozenders: de in hoofdstuk 7 beschreven evaluatie van mozaïekbeheer en een landelijke studie naar de invloed van predatie op het broedsucces van weidevogels (Teunissen *et al.*

2005). Daarbij werden in 15 verschillende gebieden in totaal 297 kievitjes en 365 jonge grutto's met een *c.* 1 g wegende zender uitgerust, waardoor een groot deel van de kuikens ook na hun dood kon worden teruggevonden. De kuikens werden gemiddeld elke twee dagen uitgepeild en geregeld teruggevangen om ze te wegen en de bevestiging van de zender te controleren. Naar vermiste vogels werd gezocht tot in de wijde omgeving van het studiegebied, onder meer in reigerkolonies en in de omgeving van bekende roofvogelnesten. De doodsoorzaak kon in een groot deel van de gevallen worden vastgesteld aan de hand van de locatie en de toestand van de overblijfselen. En kwart van alle kuikens verdween echter zonder dat resten van de vogel of de zender werden teruggevonden. Doordat we van sommige gruttofamilies naast twee van de vier kuikens ook een van de ouders hadden gezenderd, konden we vaststellen dat in het overgrote deel van die gevallen de kuikens dood moesten zijn; de ouders hielden op met alarmeren voordat ze vliegvlug hadden kunnen zijn. Vermoedelijk gaat het hier vooral om kuikens waarvan de zender door een predator is vernield of uit het zoekgebied is weggevoerd.

Als onderdeel van deze studie gingen we ook na of het aanbrengen van zenders de conditie van de kuikens negatief beïnvloedde. Bij de grutto's vonden we daarvoor geen aanwijzingen en werden in de gezinnen met een gezenderde ouder bovendien minstens zo veel gezenderde als niet gezenderde kuikens vliegvlug. Kievitjes die langer dan drie dagen een zender droegen vertoonden een 6-11% slechtere conditie dan niet gezenderde leeftijdgenoten. We weten niet of dit gevolgen had voor hun overleving maar dit valt niet uit te sluiten.

Bij beide soorten stelden we een geringe overleving van kuikens vast; tussen gebieden varieerde deze van 0-24%. Sterfte vond vooral plaats in de eerste dagen na het uitkomen van de jongen en stabiliseerde daarna rond een lager niveau om rond de vliegvlugge leeftijd verder af te nemen. Ook onder uitgevlogen jongen vond nog sterfte plaats (fig. 8.2). Predatie was de meest vastgestelde doodsoorzaak: we schatten dat 70-85% van alle omgekomen kuikens gepakt waren door predators, 5-10% omkwamen door maaiactiviteiten, en 10-20% door andere oorzaken, waaronder verdrinking in sloten, vastraken in greppels en uitputting of ziekte. Vier soorten zoogdieren en 11 soorten vogels werden vastgesteld als kuikenpredator, het vaakst daarvan Blauwe Reiger, Hermelijn en Buizerd.

Op grond van deze cijfers lijkt predatie een veel grotere tol te heffen onder kuikens dan de intensieve landbouwpraktijk. Het aandeel maaislachtoffers kan in onze studie echter iets zijn onderschat, onder meer doordat diverse soorten predators kuikens kunnen hebben opgepikt uit het pas gemaaide gras. Omdat de kans dat een kuiken als 'gepredeerd' werd gevonden niet veel groter was wanneer het perceel waar het verbleef tijdens het interval tussen twee peilingen werd gemaaid dan wanneer dat niet gebeurde, denken we echter dat zulke aaseterij niet erg veel voorkwam. Het effect van predatie kan daarnaast worden overschat als het vooral individuen treft die toch al weinig kans hadden om te overleven. Zo vonden we dat gruttokuikens met een achterblijvende conditie een grotere kans hadden om te 'verdwijnen', een categorie die vermoedelijk vooral door predatie tot stand kwam. Zo kan voedselgebrek als gevolg van intensief graslandgebruik indirect tot predatie leiden. Een andere manier waarop graslandgebruik predatiekansen kan beïnvloeden is door het wegnemen van dekking.

Gruttokuikens die verbleven op recent gemaaide of beweide percelen met kort gras liepen een twee tot drie maal zo grote kans om in het erop volgende peilinterval gepredeerd te worden (vooral door vogels) dan kuikens die in door hen geprefereerd hoog gras zaten. Gruttogezinnen die door gebrek aan ongemaaid grasland gedwongen worden op gemaaide percelen te foerageren of daar doorheen te trekken lopen daardoor een groter risico kuikens te verliezen. Deze interacties tussen agrarisch gebruik en predatie verklaarden echter maar voor een klein deel de slechte overleving van gruttokuikens, en bij Kieviten werden ze helemaal niet gevonden. Een mogelijke interactie die wij niet kunnen kwantificeren is dat wanneer intensief agrarisch gebruik de aantallen broedende weidevogels in een gebied reduceert, hierdoor voor hen de mogelijkheden afnemen om gezamenlijk predatoren uit hun nestomgeving te verjagen. Toch ligt het voor de hand dat de kolonisatie van open graslandgebieden door soorten zoals Buizerd en Vos ook zonder het versterkende effect van moderne landbouw tot een toename van de predatiedruk op weidevogels zou hebben geleid, en is het mogelijk dat predatie een bijdrage levert aan de versnelling in de afname van weidevogelaantallen die sinds de eeuwwisseling lijkt te zijn opgetreden.

Een toekomst voor Grutto's in boerenland?

In combinatie met eerdere onderzoeken laten de resultaten van de zenderstudies zien dat het broedsucces van Nederlandse Grutto's in de afgelopen decennia is gedaald, en dat dit vooral is veroorzaakt door een sterk afgenomen kuikenoverleving (fig. 7.4). Problemen van kuikens lijken daarmee de belangrijkste oorzaak van de doorgaande afname van de gruttopopulatie. De gegevens over voedselaanbod in verschillend beheerde graslanden en de positieve correlatie tussen het aandeel ongemaaid grasland in de kuikenperiode en de overleving van jonge Grutto's zijn sterke aanwijzingen dat het intensieve agrarische gebruik, met name het maaibeheer, hiervan een belangrijke oorzaak vormt. Dit is echter niet de enige factor die in de afgelopen decennia is veranderd. Samen met hoge mestgiften leidt graslandvernieuwing (jaarlijks 8% van het oppervlak in N- en W-Nederland) tot een gestage toename van kruidenarme hoogproductieve grasvegetaties met een dichte structuur waarin kuikens moeite hebben om te foerageren. Sommige roofdieren hebben zich (opnieuw) uitgebreid in het weidevogellandschap, waardoor de predatiedruk op kuikens waarschijnlijk is toegenomen. Ondertussen is sinds de jaren '80 ook het klimaat merkbaar aan het veranderen, met onder andere hogere temperaturen en in de winter en het voorjaar.

Wat klimaatverandering voor kuikens betekent is moeilijk te voorspellen, omdat dit op verschillende aspecten van hun functioneren verschillend kan doorwerken. Hogere temperaturen leiden tot minder bebroeding en lagere energieuitgaven, maar veel minder duidelijk is hoe ze de foerageermogelijkheden beïnvloeden. Daarnaast zal ook het boerenbedrijf zich aan klimaatverandering aanpassen. Zo heeft de datum van de eerste snede gras in de afgelopen 20 jaar gelijke tred gehouden met de snellere toename van temperatuursommen in het voorjaar (Teunissen *et al.* 2008). Opvallend genoeg hebben Grutto's in dezelfde periode hun broedfenologie niet aangepast, ondanks het feit dat de grotere kans dat legsels of kuikens worden uitgemaaid en het geringe aanbod van ongemaaid grasland later in het voorjaar een selectief voordeel voor vroeg broeden teweeg zouden moeten brengen, en dat de vogels tussen 1950 en 1970 hun legdatum wel hebben vervroegd (fig. 9.6). Wat de Grutto's sindsdien tegenhoudt vraagt nadrukkelijk om nader onderzoek. In ieder geval heeft het er toe geleid dat de mediane uitkomstdatum tegenwoordig later valt dan de datum waarop op 50% van het agrarische grasland de eerste snede is gemaaid. Bovendien is ook het ongemaaide grasland op het moment van uitkomen niet meer hetzelfde als twee decennia terug, maar bevindt het zich door de eerder op gang gekomen grasgroei in een verder ontwikkelingsstadium, en is daardoor minder toegankelijk voor foeragerende kuikens.

Het gezamenlijke resultaat van al deze opeengestapelde veranderingen is dat tamelijk eenvoudige beschermingsmaatregelen zoals nestbescherming en het uitstellen van maaidatums op zich niet meer voldoende zijn om de omstandigheden terug te brengen waarbij het weidevogels zoals de Grutto decennia geleden nog beter verging. De meeste praktische maatregelen in het agrarisch natuurbeheer zijn gunstig voor de succeskansen van legsels en kuikens, maar kennelijk worden ze onvoldoende intensief toegepast of zijn er belemmerende factoren die hun effectiviteit in de weg staan. Maatregelen dienen dus intensiever te zijn en tegelijk veelomvattender, om zulke belemmeringen weg te nemen. Een voorbeeld is dat aan percelen waarop uitgestelde maaidatum wordt gecontracteerd eisen moeten worden gesteld die waarborgen dat de vegetatie er een geschikte structuur heeft op het moment dat kuikens er gebruik van moeten maken, zoals een beperking van de mestgift of een hoge grondwaterstand. Dit soort aanvullende voorwaarden zal de aantrekkelijkheid voor boeren om contracten af te sluiten verminderen en de noodzakelijke financiële compensatie verhogen. Door zulke intensieve maatregelen te concentreren in gebieden met gunstige randvoorwaarden kunnen belangrijke omgevingsfactoren worden geoptimaliseerd (via de locatiekeuze of door gericht beheer), zoals planologische bescherming, landschapsstuctuur, waterpeilen, verstoring en predatie. Agrariërs hebben in zulke 'kerngebieden' een belangrijke rol te spelen in het beheer, maar natuurbescherming dient er voorop te staan en de financiële middelen om dat mogelijk te maken moeten beschikbaar zijn.

LITERATUUR

- Beintema A.J., J.B. Thissen, D. Tensen & G.H. Visser 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. Ardea 79: 31-43.
- Starck, J.M. & R.E. Ricklefs 1998. Avian postnatal development. Oxford University Press, New York.
- Teunissen, W.A., H. Schekkerman & F. Willems 2005. Predatie bij weidevogels. SOVON-onderzoeksrapport 2005/11, SOVON, Beek-Ubbergen.
- Teunissen,W.A., C. Klok, D. Kleijn & H. Schekkerman 2008. Factoren die de overleving van weidevogelkuikens beïnvloeden. Sovon-onderzoeksrapport 2008-01, SOVON Vogelonderzoek Nederland /Alterra /Vogeltrekstation, Beek-Ubbergen.
- Tjørve, K.M., H. Schekkerman, I. Tulp, L.G. Underhill, J.J. de Leeuw & G.H. Visser 2007. Growth and energetics of a small shorebird species in a cold environment: the Little Stint *Calidris minuta* on the Taimyr Peninsula, Siberia. Journal of Avian Biology 38: 552-563.
- Weathers W.W. 1992. Scaling nestling energy requirements. Ibis 134: 142-153.

DANKWOORD

Veel belangrijke dingen in het leven beginnen bij je ouders. Ik weet niet of ik niet ook tot vogelaar en onderzoeker zou zijn uitgegroeid als zij hun interesse in de natuur niet met de paplepel bij ons naar binnen hadden gegoten, maar het staat vast dat onze omzwervingen in de duinen, de fascinerende boeken thuis, en de vakanties op de Waddeneilanden en andere mooie plekken die hebben aangewakkerd en alle ruimte gegeven. Ik voel me nog steeds bevoorrecht dat ik van die passie ook mijn beroep heb kunnen maken, en ben jullie dankbaar voor zo'n mooi begin. Van het werk dat tot dit proefschrift heeft geleid heeft mijn moeder jammer genoeg zelfs het begin niet meer mogen meemaken. Mijn vader heeft veel geduld moeten opbrengen voordat hij het resultaat kon aanschouwen, maar geduld heeft hij met ons altijd gehad. Hier is het dan eindelijk!

Die vakanties op de Wadden, voortgezet in de vorm van de zomerkampen van de NJN, waren mede de aanleiding dat ik voor steltlopers als vogelgroep al vroeg een speciale belangstelling opvatte. In eerste instantie leerde ik ze vooral kennen als doortrekkers en overwinteraars, maar tijdens een doctoraalstage aan de Wulpen van het Noordhollands Duinreservaat, onder begeleiding van Jaap Mulder, kwam ik ook in aanraking met hun broedbiologie. Kuikens kwamen daar nog nauwelijks aan te pas, want die bestuderen in het onoverzichtelijke duinterrein was bijna onbegonnen werk. Bovendien raakten de Wulpen ze al snel kwijt. De vraag welke rol Vossen daarin speelden was er eentje die me jaren later opnieuw zou bezighouden bij andere steltlopersoorten.

Bij mijn introductie in 'kuikenstudies' speelde mijn oude vogelmaat Marc van Roomen een belangrijke rol. Hij was het die in 1991 een mooie kans zag om deel te nemen aan een internationale expeditie naar het Taimyr schiereiland in Siberië, een van de tot kort daarvoor nog vrijwel ontoegankelijke broedgebieden van onze overwinterende steltlopers en ganzen, en mij mee vroeg. We arriveerden pas halverwege het broedseizoen en 's avonds laat in de overdonderend mooie toendra, waar Les Underhill zich meteen over ons ontfermde. "Let's go off into the field right now, the first Curlew Sandpiper nests will hatch tonight and weather as fine as this never lasts for long here". Les, thanks a lot for your company and hospitality back then in the tundra and over the following years. In de weken die daarop volgden deden we het veldwerk dat heeft geleid tot hoofdstuk 4 en groeide mijn fascinatie voor wat steltloperkuikens allemaal klaarspelen. Toen ik een half jaar later de mogelijkheid kreeg om te solliciteren op een aio-baan aan zulke steltloperkuikens, maar dan in Nederlandse graslanden, greep ik die dan ook aan.

Die aio-plek was tot stand gekomen door de inspanningen van Albert Beintema, weidevogelonderzoeker bij het RIN (later IBN-DLO, weer later Alterra) die inzag dat de ecologie van kuikens wel eens cruciaal kon zijn bij de problemen die onze weidevogels ondervinden. Hij startte hieraan diverse onderzoeksprojecten, waarvan er een uitmondde in het promotieonderzoek van Henk Visser aan de warmte- en energiehuishouding van opgroeiende kuikens. Toen die door Henk in het laboratorium nauwgezet waren uitgezocht, was het tijd om weer in het veld te gaan kijken wat dat in de praktijk betekent voor een kuiken dat moet opgroeien in modern grasland dat door boeren intensief wordt bemest en gemaaid. Dit project werd gefinancierd door de Dienst Beheer Landbouwgronden van het ministerie van LNV, en vanuit die dienst begeleid door Maaike Bruggink, Joep van de Laar en Dick Melman, terwijl ik onder de supervisie van Rudi Drent was aangesteld bij de Rijksuniversiteit Groningen.

Dagelijkse begeleiding en adviezen kreeg ik vooral van Albert en Henk. Een aantal van Albert's ideeën zijn cruciaal geweest voor onderzoek, zoals het gebruik van de enclosures om gruttofamilies in detail te bestuderen. Toen ik eens verzuchtte dat het waarnemen van foeragerende kuikens onder contrasterende beheersomstandigheden zwaar werd gefrustreerd doordat grutto-ouders helder voor ogen hebben wat goed grasland voor hen is, vroeg hij of we het niet zonder die ouders zouden kunnen doen. Dat heeft geleid tot het foerageerexperiment in hoofdstuk 6. Henk heeft altijd met grote belangstelling meegedacht in het project, en bracht elk jaar een aantal velddagen door in Baarn. Hij had een belangrijke inbreng vanuit zijn belangstelling voor de energetische kant van het onderwerp en zijn positie bij het Centrum voor Isotopenonderzoek in Groningen. Zonder zijn inzet zouden de metingen aan energieuitgaven van grutto- en kievitkuikens, maar ook die aan Kanoeten en Kleine Strandlopers, niet mogelijk zijn geweest. Dat die inzet zich niet tot mijn onderzoek beperkte blijkt wel uit het overzicht van zwaar water studies aan kuikens in tabel 9.1: Henk heeft een grote rol gespeeld in het vooruitbrengen van onze kennis van de energetische kosten van verschillende manieren van opgroeien bij vogels. Het is erg jammer dat hij de afronding niet meer kan meemaken, maar ik ben blij dat zijn rol toch nog tot uitdrukking gebracht kon worden in het co-promotorschap.

Natuurmonumenten, met name beheerder Rik Niewerf, verleende toestemming voor en praktische hulp bij het onderzoek in een van hun weidevogelreservaten in het Eemland bij Baarn. Aan de 'boerenkant' van het onderzoeksgebied was ik te gast bij de familie Van Rossenberg. Ook letterlijk, want vier voorjaren lang vond ik onderdak op het erf van hun boerderij, waar ik een van de fameuze RIN-caravans mocht neerzetten en ook nog een stal werd ontruimd als extra slaap- en opslagruimte. Het was fantastisch hoe zij de drukte tolereerden die mijn verblijf en dat van de diverse helpers in het onderzoek met zich meebrachten. In de eerste plaats moet daarvan Leo van den Bergh genoemd worden, die meehielp met het zoeken van nesten en met de bemon-

steringen, en die met zijn verhalen zorgde dat zelfs het uren vergende uitpluizen van bodemmonsters nooit saai werd. Karen Krijgsveld, Arjan Boele en Jeroen Postema waren ook onmisbaar – als hulp en als gezelschap – doordat zij als doctoraalstudent hele veldseizoenen meedraaiden. Arjan rondde geheel eigenhandig het veldwerk af toen ik eind juni naar een tweede voorjaar in de toendra vertrok. Daarnaast brachten studenten van de dieroecologiecursus in Groningen voor kortere perioden een hoop extra werkkracht en gezelligheid mee: Martjan Lammertink, Suzan van Lieshout, Nelly Swijnenburg en Odette Vervoort. Zonder hen zouden we niet zoveel aaneengesloten registraties van de dagelijkse activiteiten van gruttofamilies hebben kunnen doen. Andere geregelde helpers in die tijd waren Marianne Kroglund, Marc van Roomen en Ingrid Tulp.

Ik deed dit werk vanuit het Instituut voor Bos- en Natuuronderzoek in Arnhem, waar 'de koffietafel' en de vogelgroep met Albert, Allix Brenninkmeijer, Bart Ebbinge, Jaap Graveland, Arie Spaans, Eric Stienen, Wolf Teunissen, Ben Verboom ('nachtvogels') en Jan Veen voor inspiratie zorgden. Vooral aan discussies over het werk aan sternenkuikens met Eric en Allix, en de door Arie geëntameerde 'grafiekenborrels' heb ik goede herinneringen. Henk Siepel, Ruud van Kats en Dennis Lammertsma waren behulpzaam bij het bemonsteren en determineren van de insecten, en Jos Bodt bij het determineren van regenwormen.

Prachtig was het dat ik in de gelegenheid werd gesteld als onderdeel van mijn project opnieuw onderzoek te doen aan in de toendra opgroeiende kuikens, dit maal aan Kanoeten langs de noordkust van Taimyr. Hoewel (alweer) een vos roet in het eten gooide lukte het onze ploeg bestaande uit Petra de Goeij, Joop Jukema, Jan van de Kam, Theunis Piersma, en Ingrid Tulp met de nodige inspanning en ontberingen toch een mooie dataset bij elkaar te sprokkelen, die zijn weerslag heeft gevonden in hoofdstuk 3.

Na het aflopen (afronden is niet het juiste woord) van mijn aio-schap kon ik in een tijdelijke aanstelling (die bij de reorganisatie van IBN-DLO tot Alterra werd omgezet in een vaste) de ervaring de we in Taimyr hadden opgedaan met het zenderen van Kanoeten gebruiken om de omzwervingen en perceelvoorkeur van gruttofamiles te volgen. In de paar jaar daarna volgden meer van dat soort studies, in relatie tot nieuwe typen beheersovereenkomsten zoals de 'ruime jas' en vluchtstroken, veelal samen met Gerard Müskens. Wolf Teunissen was ondertussen bij SOVON neergestreken, en is sindsdien mijn vaste onderzoekspartner en praatpaal op (onder andere) weidevogelgebied geworden. We werkten onder andere samen in de twee grote weidevogelprojecten waarvan in hoofdstukken 7 en 8 resultaten zijn opgenomen. In het predatieonderzoek kwam ik de Vossen weer tegen, maar niet zo vaak als velen hadden verwacht. We werkten daarin verder samen met Aad van Paassen die een belangrijk deel van de coördinatie en fondsenwerving voor zijn rekening nam, geen geringe klus gezien het grote aantal betrokken organisaties. In 'Nederland Gruttoland' werkten we verder samen met Ernst Oosterveld van onderzoeksbureau Altenburg & Wymenga. Ook in die projecten waren veel mensen bij het (peil)werk in het veld betrokken: veldmedewerkers Leo van den Bergh, Karen Bouwman, Yde van der Heide, Martin de Jong, André van Kleunen, Mark Kuiper, Frank Majoor, Gerard Müskens, Henk-Jan Ottens en Frank Willems, en studenten Laura Beskers, Ineke Geelen, Piet Heemskerk, Bennie Henstra, Helene de Jong, Willem Nell, Karel Pieter Plas, Tijmen Meijer, Eefje Vromans en Felix Weijdema. Vooral de beide Franken en Piet hebben heel veel werk verzet. Kees van 't Hoff en Theo Gerrits van Microtes hebben hard hun best gedaan om ons steeds te voorzien van zenders. Daarnaast hebben vele personen, waaronder veel boeren en vrijwillige weidevogelbeschermers, toestemming verleend hun land te betreden, nesten gezocht, contacten gelegd of anderszins meegeholpen. Het onderzoek voor 'Nederland Gruttoland' werd begeleid door Gerrit Gerritsen, Hans Krüse, Aad van Paassen en Nerus Sytema, en door een auditcommissie bestaande uit de professoren Frank Berendse, Theunis Piersma en Geert de Snoo.

Nadat deze twee grote projecten waren afgerond was ik van plan de tijd te nemen om nu echt het proefschrift te gaan afmaken. Toen deed zich echter de mogelijkheid voor om als onderzoeker te gaan werken bij het Vogeltrekstation op het Nederlands Instituut voor Ecologie. 'Opgegroeid' als ik was op de vinkenbaan van Castricum kon ik daar geen nee tegen zeggen. Ik heb geen spijt van die overstap, dankzij het veelzijdige werk en de prettige nieuwe collega's Woutéra van Andel, Gert Speek en Henk van der Jeugd. Op het NIOO kreeg ik van Louise Vet en Hans van Veen gelukkig de gelegenheid om mijn proefschrift verder af te maken; zonder die tijd was dit boekje er nu nog niet geweest. In de schrijffasen liet ook mijn oorspronkelijke promotor Rudi Drent zich van zijn beste kant zien, door steeds vlot te reageren op nieuwe versies van stukken, en altijd met zinvolle suggesties. Doordat het zo lang heeft geduurd kan hij zelf geen promotor meer zijn, maar juist ook in de laatste fasen heb ik veel aan hem gehad. Dat Theunis nu het stokje van het promotorschap van hem overneemt is eigenlijk best passend gezien zijn bemoeienissen in verschillende fasen van mijn weidevogelloopbaan, waaronder de Nederland-Gruttoland studie, en ons gezamenlijke Kanoetenwerk in Siberië.

Ik ben erg blij met de wijze waarop Nicolet Pennekamp dit proefschrift heeft opgemaakt, en met het resultaat. Dick Visser heeft in korte tijd de figuren vervaardigd. De fotografen van wie ik enkele foto's mocht gebruiken wil ik ook hartelijk bedanken: Harvey van Diek, Jan van de Kam, Henk-Jan Ottens en Wolf Teunissen. Verder ben ik blij dat Frank Berendse, Åke Lindström en Marcel Klaassen in de leescommissie plaats wilden nemen.

Ingrid Tulp heeft, niet alleen als geregelde veldhulp in Baarn en als mede-onderzoeker in Siberië, zowel bij de Kanoeten als tijdens ons latere gezamenlijke werk in Medusa Bay, maar ook aan het thuisfront een grote rol gespeeld bij het tot stand komen van dit proefschrift. Niet in de laatste plaats door me met regelmaat op te jutten er weer mee verder te gaan. Het gereedkomen van haar eigen proefschrift was natuurlijk ook een niet te missen stimulans! Ik vind het prachtig dat we ons nu weer samen met nieuwe dingen kunnen gaan bezighouden.

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