Travels in a changing world

Flexibility and constraints in migration and breeding of the barnacle goose

The work reported in this thesis was carried out at the Centre for Ecological and Evolutionary Studies of the University of Groningen, The Netherlands.

The research was financially supported by scholarships from the Marianne und Dr. Fritz Walther-Fischer Fund, Germany, and the Ubbo Emmius Fund of the University of Groningen. Additional support was provided by the Arctic Programme of the Netherlands Organisation for Scientific Research (NAP-NWO), the Schure-Beijerinck-Popping Funds of the Royal Dutch Academy of Sciences (KNAW) and the European Science Foundation. Production of this thesis was partly funded by the Faculty of Mathematics and Natural Sciences of the University of Groningen.

Lay-out and figures: Dick Visser
Cover drawing: Jens Gregersen
Photographs: Götz Eichhorn, unless stated otherwise
Printed by: Van Denderen BV, Groningen

ISBN: 978-90-367-3449-3
ISBN: 978-90-367-3448-6 (electronic version)

RIJKSUNIVERSITEIT GRONINGEN

Travels in a changing world

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Proefschrift

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. F. Zwarts,
in het openbaar te verdedigen op
maandag 23 juni 2008
om 14.45 uur

door

Götz Eichhorn

geboren op 15 november 1972
te Neuhaus/Elbe, Duitsland

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Умом Россию не понять,
Аршином общим не измерить.
У ней особенная стать,
В Россию можно только верить.

Ф. И. Тютчев (F.I. Tyutchev), 28 November 1866

You will not grasp her with your mind
Or cover with a common label,
For Russia is one of a kind -
Believe in her, if you are able...

Translation by A. Liberman (2003) in *Russian Life* 46: 32-34

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Aerial view of our Russian field site at Kolokolkova Bay.

Chapter 1

General introduction

Götz Eichhorn

The management of time and energy

All processes of life require energy and nutrients, and the efficiency at which organisms exploit and utilise these resources has direct consequences for individual fitness (survival and reproduction). Resource demands vary during the annual cycle, with periods of reproduction taking a central position when supplies are needed not only for parents but, in addition, for the growing offspring. Furthermore, most habitats show notable seasonal fluctuations in the availability of resources. Therefore, there is strong selection pressure on the tuning of pulses of resource demands to pulses of availability (Lack 1968). Maximising fitness to a large extent means optimising management of time and energy (Cuthill and Houston 1997). Different phylogenetic background and morphological, physiological and behavioural capabilities of animal species inhabiting different environments lead to the development of a great variety of solutions to the same problem.

However, it has become clear that this optimisation process largely acts at the level of the individual. The combined reproductive value, including offspring and adult survival, is maximised by birds timing their breeding season according to their own capabilities and local environmental circumstances ('individual optimisation hypothesis', e.g., Drent and Daan 1980; Daan and Tinbergen 1997; Brinkhof et al. 2002; Drent 2006). It will be crucial to account for the combined survival prospects of both adults and young, because while the latter usually benefit from earlier breeding (Rohwer 1992; Drent 2006), parents may have to pay the costs of laying too early through reduced survival (Brinkhof et al. 2002). Nevertheless, the general conclusion from supplementary feeding experiments (Nager 2006) is that early spring food bottlenecks to some extent constrain birds from laying earlier, forcing them to delay breeding until they reach an optimal nutritional state that is needed for starting a breeding attempt (Perrins 1970). Adequacy of breeding condition is determined by a number of factors, among them are: patterns of parental care (uni- or biparental), mode of development (precocial or altricial), fasting endurance (which increases with body size) and risk of predation, which, furthermore, interact with environmental factors like climate, diet and food availability (Moreno 1989).

Cost and benefits of avian migration

The flight skills of birds enable them to integrate resources over vast geographical areas, and bird migration may be regarded primarily as an adaptation for exploiting seasonal peaks of resource abundance and avoiding seasonal resource depression (Alerstam et al. 2003). Migrants may take advantage of the spatial progression of resource peaks along a climatic gradient. For Arctic-breeding geese it has been proposed that they schedule their spring migration according to the 'green wave' of the (most digestible) early spring growth of grass along the flyway and gradually store body reserves based on the food they encounter at each site (Drent et al. 1978; Van der Graaf et al. 2006b). By bringing stored resources (notably fat and

protein) for egg formation with them to the breeding grounds migrants can finally get ahead of the wave of seasonal food abundance, enabling them to better match the brood-rearing period to the local resource peak (Perrins 1970; Drent 2006). In this way, migrants can circumvent the nutritional bottleneck preventing them from laying earlier as outlined above. The strategy of importing resources for reproduction to the breeding grounds has been termed 'capital breeding' and contrasted with 'income breeding', which refers to the reliance on current intake to meet the nutrient and energy demands of reproduction on the spot (Drent and Daan 1980). Recent evidence suggests the predominance of a mixed capital-income strategy for most arctic migrant birds, with the potential for capital breeding increasing with body size (Meijer and Drent 1999; Klaassen 2003; Drent et al. 2006).

However, benefits are balanced by associated costs. Adding migratory episodes to the annual cycle comes at the expense of both extra time and energy, and involves critical adjustments in the general management of these resources (Kokko 1999; Drent et al. 2003). Accordingly, time and energy are the assumed major currencies for the selection of a certain migratory strategy (Alerstam and Lindström 1990). Most of the empirical evidence so far supports the assumption of time-selected migration, reflecting the enhanced time pressure migrants face due to the overall tighter annual schedule (Hedenström 2007). However, in practice it may be often difficult to disentangle the relative importance of these theoretically distinct currencies. Due to predation or other hazards encountered during the journey, migration may take a high toll compared to other phases in the annual cycle (Sillett and Holmes 2002; Newton 2006; Newton 2007). Many migrants rely on multiple and very specific stopover sites for refuelling. This dependency renders them vulnerable to deterioration or disturbance at such crucial stepping stones (Béchet et al. 2004; Baker et al. 2004; Klaassen et al. 2006a; Jefferies and Drent 2006).

Motivation and scope of the thesis

This thesis investigates aspects of timing and resource acquisition and utilisation in the barnacle goose *Branta leucopsis* during spring migration and reproduction. It aims to contribute to our understanding of causes and constraints of migratory decisions in animals. The barnacle goose population wintering along the Wadden Sea coast from the Netherlands to Denmark, and traditionally migrating via a stopover in the Baltic to its breeding sites in northern Russia (Fig. 1.1), is outstanding in at least three characteristics.

First: since a population low at ca. 20 000 birds in the 1950s the total flyway population has grown exponentially to more than half a million birds at present. Second: since the early 1990s an increasing share of the population delays its departure from the wintering quarters in the Wadden Sea by about four weeks. Third: long being regarded as an obligate Arctic breeder, within the past three decades this species has successfully colonised a wide variety of habitats at temperate latitudes, thereby shortening the migratory distances considerably or refraining from migra-

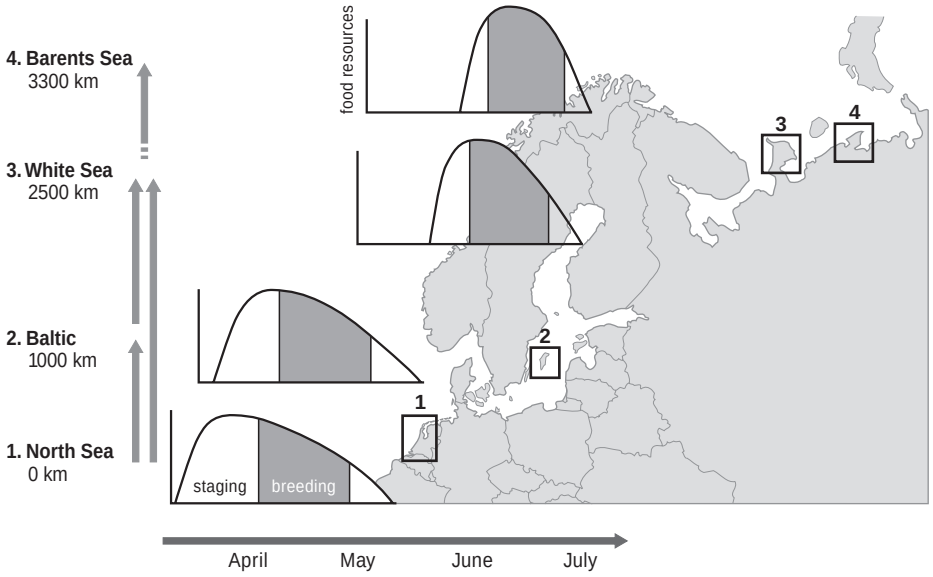

Figure 1.1. Barnacle geese wintering along the North Sea coast are expected to schedule their spring migration and reproduction according to resource peaks. These resource peaks progress along a climatic gradient from south to north. While the peaks may increase in amplitude, the time window allowing the deposition of body stores and raising young becomes increasingly shorter. Fieldwork for this thesis has been conducted at following sites (marked out on the map by squares): 1. in the Dutch Delta (breeding) and on the island of Schiermonnikoog (staging period); 2. on and near the island of Gotland (breeding); 3. on Kanin Peninsula (staging); 4. in breeding colonies at the Kolokolkova Bay.

tion altogether. Moreover, this expansion seems contradictory to an expected northward shift as a response to global warming. These remarkable changes raise questions about the flexibility of migratory and reproductive schedules. What are the costs and benefits of different migration strategies? And, given the context of global change, to what extent are animals capable of adapting to rapidly changing environments?

Although it is now widely recognised that migration and reproduction are tightly interlocking events (Drent et al. 2006), the monitoring of the progress of avian long-distance migration at individual level and its linkage to events in the breeding phase has so far only rarely been achieved (Madsen 2001; Bêty et al. 2003; Alerstam 2006a; Drent et al. 2007). The present thesis attempts to bridge this research gap for the migratory barnacle goose population breeding in the Russian Arctic. The other central theme in this thesis is a within-species comparison of major life-history traits in populations breeding along a large ecological gradient from arctic to temperate environments exerting different selection pressures. For instance, intra-specific studies on the use of nutrient-stores seem necessary in order

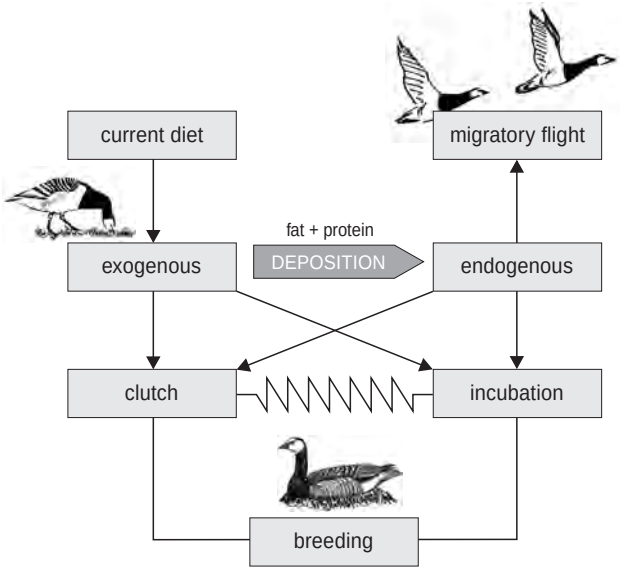

Figure 1.2. Barnacle geese deposit (endogenous) body stores (mainly fat and protein) in preparation of and during migration. Body stores are needed for the migratory flight itself and for subsequent reproduction, when the female has to allocate these stores to clutch production and incubation. Nutrient and energy demands during reproduction are supplemented by (exogenous) food resources at a degree depending on local environmental conditions.

to verify and better understand the different tactics of reproduction evolved in waterfowl, but have been scarcely conducted so far (Rohwer 1992; Alisauskas and Ankney 1992a; Esler et al. 2001). Figures 1.1 and 1.2 illustrate the framework of this thesis.

Introducing the study populations

With the aim of comparing the solutions achieved by long- and medium-distance migrants as well as resident populations within one species in meeting the demands of their breeding schedules, barnacle geese were studied at three breeding sites along the flyway as depicted in Fig. 1.1. As representative for the ancestral long-distance arctic-breeding population, a colony on the Russian coast has been studied intensively every summer since 2003. The newly established resident population in the Netherlands studied 2004-2006 provides the maximum contrast, and the third site in Sweden concerns the island population of Gotland studied intensively by Larsson and his team during the past twenty years. Our own investigations on Gotland were conducted during the incubation phase in 2000, 2003 and 2004. Details on these study sites are appended to this chapter.

Although the Baltic and Dutch populations have been growing rapidly since their establishment in 1971 and 1981, respectively (Larsson et al. 1988b; Meininger and Van Swelm 1994) now together numbering 46 000 individuals, the Russian arctic breeding population is by far the most numerous, currently representing 90% of the common wintering population of more than 500 000 birds (Black et al. 2007). All recently established breeding areas are situated within the flyway, i.e. they are confined to historical wintering areas and staging grounds of the species. Following individual birds from these study populations was made possible by marking them with engraved coloured leg rings, readable by telescopes. For this purpose we colour-ringed approximately 1400 birds in the Barents Sea between 2002 and 2005, and 420 birds from the Dutch population in 2004 and 2005. In the Baltic about 5500 birds were colour-ringed between 1984 and 2000 by Swedish colleagues (K. Larsson and co-workers).

Life history of the barnacle goose

The barnacle goose is a long-lived, socially and genetically monogamous species with biparental care (Black 1996). Ebbinge et al. (1991) estimated a mean annual survival rate of adult birds belonging to the 'Baltic-Russian flyway population' of 90% corresponding to a mean life expectancy of nine years (Seber 1982) but life spans of more than 20 years have been frequently recorded (Ebbinge pers. comm.). Final pair formation and first breeding takes place at 2-3 years of age, often preceded by a number of trial liaisons with potential partners (Van der Jeugd and Blaakmeer 2001). The pair stays together year-round and usually throughout life. For geese from the Baltic breeding population Forslund and Larsson (1991) measured an annual divorce rate of 2.4%. Barnacle geese breed in colonies. Most clutches contain 3 to 6 eggs, from which the precoccial offspring hatches after an incubation period of 24 to 26 days (Owen 1980; Dalhaug et al. 1996). The duty of incubation is carried solely by the female, while the male takes an important role in the defence of nesting and feeding grounds and protection of offspring against predator attacks (mainly from larger gulls, skuas and foxes). Being obligate herbivores of relatively small size, barnacle geese rely on forage of high nutrient content and digestibility, and still, they spend most of the daylight feeding in order to gather and process the necessary amounts of plant food (Prop 2004). The geese feed predominantly on grasses, sedges and herbs utilising coastal salt marshes as their traditional feeding habitat. However, like many other waterfowl, barnacle geese have increasingly utilised improved grassland during the past 20 years, where forage quality is enhanced due to intensive agricultural fertilization (Van Eerden et al. 2005). It has been argued that, despite the apparent attractiveness to geese, forage from cultivated grassland provides them with a less favourable composition of nutrients compared to food from salt-marsh habitat, thereby affecting the composition of body stores deposited during spring feeding and finally impairing breeding success (Prop and Black 1998; Prop and Spaans 2004).

In this thesis I focus on the adult, reproductively mature, female barnacle goose. First of all because of the central role the female goose plays in the context of time and resource management for reproduction (Fig. 2). Secondly, in geese it is mainly the female who chooses the breeding site. Females prefer to breed in their natal colony close to kin and/or at sites where they bred successfully before (Rohwer and Anderson 1988; Van der Jeugd et al. 2002). Northern geese have been subject to long-standing and intensive ecological study, which is testified by the impressive compilation in Batt et al. (1992). The overviews by Afton and Paulus (1992), Alisauskas and Ankney (1992a), and Rohwer (1992) for waterfowl in general, and the very recent compilation by Black et al. (2007) for the barnacle goose provide a baseline for comparison with my project. Valuable insights from the interface of migration and reproduction through long-term observation of individually marked birds come also from studies on greater snow goose (Bêty et al. 2003; Gauthier et al. 2003), emperor goose (Schmutz et al. 2006), pink-footed goose (Madsen 2001; Klaassen et al. 2006a) and the barnacle goose population breeding on Spitsbergen (Prop et al. 2003). Finally, I can build on findings from van der Graaf (2006) who investigated the interactions of barnacle geese and their food plants along the same flyway.

Outline of the thesis

After an introduction to study sites and study populations at the end of this chapter, the thesis is further divided into three major parts, followed by a general discussion of the overall findings.

Part I: Tools and techniques
Technological progress offers exciting opportunities to study wild animals in their natural environment. Part I describes the techniques we used to follow individual birds through space and time, and to study their acquisition and use of body stores. **Box A** informs about the two remote tracking systems we used to monitor the long-distance migratory journeys of individuals breeding in the Russian Arctic: satellite telemetry using implanted transmitters and global location sensing (GLS) using archival tags attached to the legring. These remote tracking techniques were supplemented by an extensive ringing program, involving all three study populations. Direct observations on marked birds provided us with information about survival rates and individual performance on the breeding grounds (timing, condition, clutch size, breeding success). In **chapter 2** we calibrate and evaluate an isotope dilution method as non-destructive means to estimate total body water, fat and fat-free mass in the barnacle goose. **Box B** provides details of carcass composition at the organ level.

Part II: Travel to breed
The first spring travel itineraries of females from the Russian breeding colony equipped with GLS tags were gathered in 2004 and are presented in **chapter 3**.

Most of our tracked birds delayed their departure from the wintering grounds in the Wadden Sea considerably (by up to ca. four weeks) compared to mass departures in former times. An important finding was that the staging duration in the Baltic was reduced according to the delay of departure from the Wadden Sea, but that all birds spent a remarkably consistent time period (ca. three weeks) in arctic pre-nesting staging sites. In **chapter 4** we investigate the change in spring migratory routines in more detail using long-term data on spring migration counts, population counts and temperature data. We also employ an analytical model based on optimal migration theory to evaluate conditions of 'fuel deposition' rates when bypassing the Baltic may become beneficial. Data collated from GLS or satellite tracking over two seasons (2004 and 2005) allowed us further to examine the within-individual variability of spring travel itineraries between years, and if alternative migration strategies may incur differences in the timing of breeding. **Chapter 5** reviews the importance of spring stopovers for reproductive prospects in Arctic-nesting geese. We emphasise the resource demands needed to successfully complete incubation, which exceed by far (additional) requirements to form the eggs. These total demands cannot be met solely by feeding at the breeding grounds but must be supplied to a significant part by body stores accumulated at pre-breeding staging sites.

Part III: Why travel to breed: arctic and temperate-breeding compared

In this section we compare three breeding populations of the barnacle goose along the Baltic-Russian flyway, one arctic (Barents Sea) and two temperate (Baltic, North Sea). In **chapter 6** the focus is set on the timing of reproduction in relation to subsequent offspring production. We show that timing of breeding in the arctic population coincides with the period of maximal offspring production, whereas temperate populations currently seem not completely adapted to their novel environment. We reason that there must be constraints preventing earlier breeding and moulting in the temperate area. Nevertheless, survival of young until arrival in the wintering areas (estimated by mark-recapture techniques) is much lower for the arctic birds pointing at risks of migration.

Incubation is a time of great nutritional stress to the female, when she, constrained by her egg-caring duties, has to draw substantially from body stores. The female supplements her resource needs by feeding during incubation recesses. In **Box C** we examine frequency and duration of feeding recesses in relation to day of incubation for females from the Dutch breeding colony. We also compare total daily recess time of Dutch females to arctic-breeding females from the Barents Sea population. In **chapter 7** we concentrate on resource utilisation during reproduction. Temperate breeding barnacle geese loose more body mass during incubation than their arctic conspecifics. We further distinguish between depletion of fat and protein stores during incubation with the help of isotope dilution measurements (method evaluated in chapter 2) and show that temperate breeders exhaust their protein stores to a larger extent than arctic-breeding barnacle geese. We also demonstrate the existence of opposite latitudinal gradients in clutch size and egg size, with clutch size increasing from north to south.

In **Box D** I examine the deposition of body stores during spring staging in two different feeding habitats, agricultural pasture and salt marsh, differentiating between fat and protein storage. In the final **chapter 8** I integrate findings from the previous chapters supported by supplementary information. The acquisition of body stores receives special attention. A comparison of historical and current data on body mass dynamics of barnacle geese supports the notion that fuelling prospects in the Wadden Sea have improved over past decades. In the discussion around food utilisation from agricultural pastures versus natural habitat an unresolved problem concerns the different nitrogen retention efficiencies found for these two feeding habitats. I end with a view on perspectives for the barnacle goose study, which provides a well suited study system for more research into the mechanisms of adaptation to lifestyles at different latitudes thereby deepening our understanding of how organisms may cope or fail to cope with the challenges of global change.

Details on study populations and study sites

In the Russian Arctic

Traditional breeding areas were restricted mainly to the islands of Novaya Zemlya and Vaygach in the eastern Barents Sea. Through expansion back down the flyway, since the 1980s breeding occurs now up to the eastern White Sea coast, 650 km westwards from the traditional sites (Filchagov and Leonovich 1992; Syroechkovsky Jr. 1995; Litvin unpubl. data, see Fig. 1.3). Present numbers along the Western Barents Sea coast, including the island Kolguev, are not well known, but are likely to exceed 60 000 breeding pairs (Anisimov et al. unpubl.). Our study colony is situated on the Kolokolkova Bay salt marshes, Malozemelskaya Tundra, on the west coast of the Pechora Delta, adjoining the nearly abandoned village Tobseda (68°35'N, 52°18'E) on a peninsula bordered by the Barents Sea to the north and the Kambalnichya Pakha Gulf of the Kolokolkova Bay to the south. The colony comprises a varying number of breeding sites hosting between 1200 and 2000 breeding pairs in total, including up to 1000 pairs on islands in the north of the bay 5 km off the

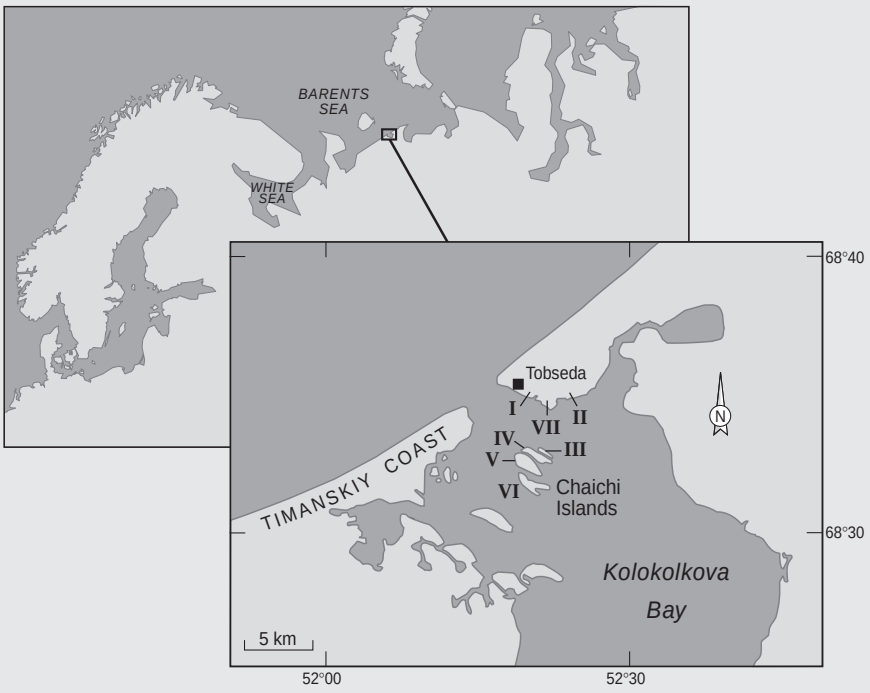

Figure 1.3. Map showing the location of the study area in the Kolokolkova Bay. Roman numbers indicate the locality of barnacle goose breeding sites.

coast (Fig. 1.3). Van der Graaf et al. (2004) describe the habitats and their use by geese (small numbers of White-fronted *Anser albifrons* and Bean *Anser fabalis* Geese also nest). Barnacle geese have bred in the study area since at least 1994 (Syroe chkovsky Jr. 1995). Data from this site were mainly gathered during field expeditions in 2003 to 2005.

In the Baltic

In 1971, the first breeding pair in the Baltic was found (Larsson et al. 1988a), and since then this population has grown at a spectacular rate, numbering 17 000 individuals in 1997 (Larsson and Van der Jeugd 1998) and approximately 21 000 individuals in 2005 (Black et al. 2007; Larsson unpublished). In the Baltic, birds have been studied mainly in the oldest and largest breeding colony situated at Laus holmar (57°17'N; 18°45'E) off the east coast of the

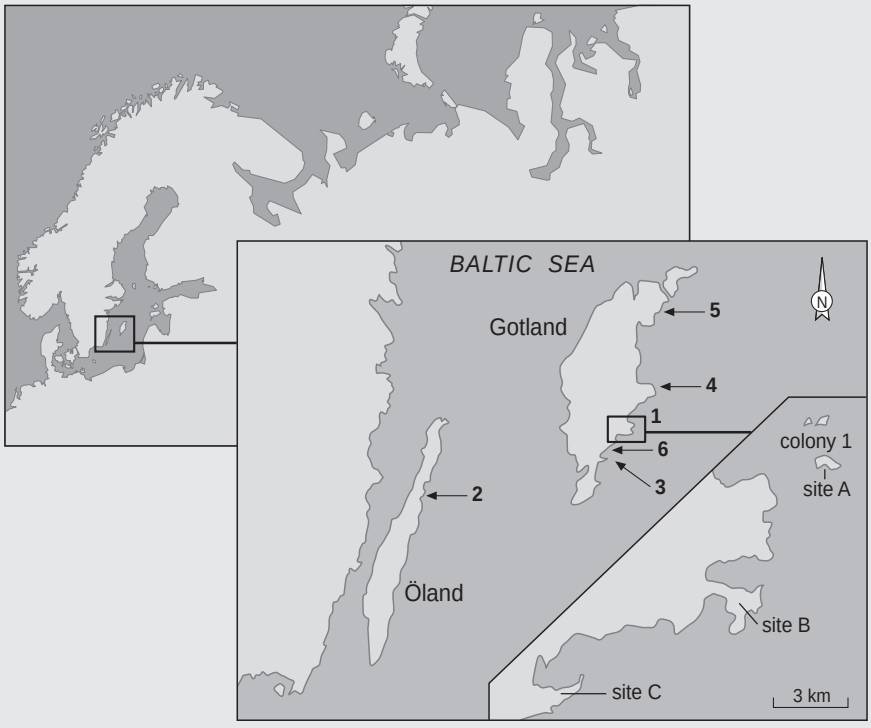

Figure 1.4. Map showing the location of the 6 largest barnacle goose colonies that were subject to long-term studies in the Baltic (numbers 1 to 6 in large lower panel) with the oldest and largest colony 1 serving as main study site (small lower panel). This colony consists of three breeding islands and three major brood-rearing areas; sites A, B and C. From van der Jeugd (1999).

island of Gotland, Sweden, from 1984 to 2006 (Larsson et al. 1988a; Larsson and Forslund 1994; Larsson et al. 1998). During the 20-year study period, this colony increased from 450 to a maximum of 2450 breeding pairs. During recent years, the number of breeding pairs has declined due to predation and disturbance by red foxes and white-tailed eagles. In addition to this colony, five other Baltic colonies have been studied less intensively during the same period (see Fig. 1.4 for location). A more detailed description of the study area can be found in Larsson et al. (1988a) and van der Graaf et al. (2006a; 2007a). We studied body mass of incubating geese in this population in 2000, 2003 and 2004. For analyses on the timing of reproduction and clutch size we could make use of the long-term data set collated by K. Larsson and co-workers since 1984.

Data on spring staging numbers of barnacle geese in Estonia were gathered by our local colleagues. Birds were counted by ground surveys in 1964, 1968, 1970 and from 1974 onwards by aerial surveys (in 16 years during 1974 – 2005). Aerial censuses were conducted in the period 5-15 May using a constant census area and routine over the years (Leito 1996). Recently established staging sites in northern Estonia were not surveyed by airplane but visited frequently from the ground. However, aerial census coverage of stopover sites hosting 100 or more geese regularly has been nearly 98% until year 2000 and has been still about 95% since then.

Furthermore, census data on geese passing through the Baltic in spring has been collected by the Ottenby bird observatory (56°12'N, 16°24'E) located at the southern tip of the Swedish island Öland and by the Kymenlaakso Birding Society for passage over the Gulf of Finland (counting post near Kotka: 60°28'N, 26°58'E).

The North Sea

The stronghold of the North Sea breeding population is established in the southwest of the Netherlands (Meininger and van Swelm 1994; Ouweneel 2001). Here, the first breeding pair was encountered in 1981, and this population has also been growing rapidly since then, numbering 25 000 individuals in 2005 (van der Graaf et al. 2006a; Voslamber et al. 2007). We studied barnacle geese at Hellegatsplaten, the Netherlands (51°42'N, 4°20'E), one of the largest colonies in the Delta area in the southwest of the country between 2004 and 2006. This colony consists of several breeding sites, mostly situated on islands (see Fig. 1.5). The total number of nests varied between 518 and 537 during the three study years.

We studied spring staging barnacle geese (preparing for migration to Russian Arctic or Baltic breeding sites) on the Dutch barrier island Schiermonnikoog (53°30'N, 6°10'E) in 2004. Here the geese utilise two major habitats: natural saltmarsh and intensively cultivated grassland (for details see Bos

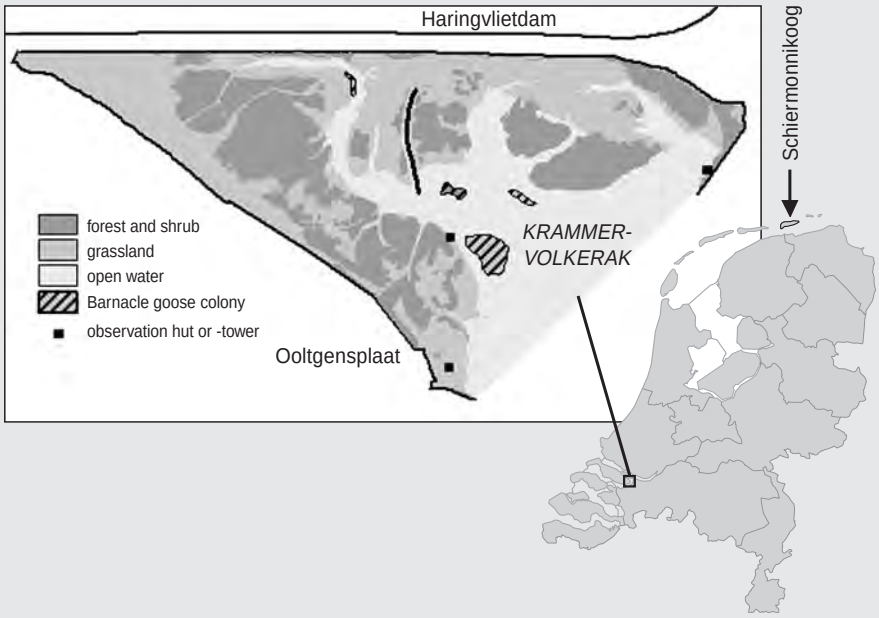

Figure 1.5. Map showing a major Dutch barnacle goose breeding site at Hellegatsplaten in the Delta area in the southwest of the Netherlands. Most (but not all) geese nest on (often wooded) islands. The study site for staging geese on the island Schiermonnikoog is marked by an arrow.

and Stahl 2003). Finally, data on the timing of spring mass migration from the Wadden Sea were collated in the north-eastern Wadden Sea in Schleswig-Holstein, Germany (ca. 54°36'N, 8°52'E), by Stock and Hofeditz (2002), Koffijberg and Günther (2005) and Koffijberg (pers. comm.).

Our means of transport in the Arctic.

Part

I

Tools and techniques

Box

A

Tracking migratory geese

Götz Eichhorn

Tracking devices

We used two techniques to track annual movements of female Barnacle Geese nesting at the Tobseda colony: global location sensing and satellite telemetry. The **global location sensing (GLS) approach** is based on the principle of geolocation by light levels (Wilson et al. 1992). Light-sensitive archival tags equipped with an inbuilt clock record ambient light levels from which both dusk and dawn events are estimated. These are used to calculate geographical positions (two fixes daily): day (night) length determines latitude and time of local midday (midnight) determines longitude. Each 9 g tag (produced by the British Antarctic Survey) was attached to one of our standard plastic leg rings (inscribed with an individual code, see picture in chapter 3). The total mass of the logger and all 3 rings (two inscribed colour plastic rings and one stainless steel numbered ring from the Ringing Centre in Moscow) was 21 g, corresponding to 1.5% of the average female body mass at the end of incubation, the leanest period in the annual cycle. The GLS units (54) were attached to the geese during their breeding/moulting period in 2003 and retrieved in subsequent seasons (24 and 12 units in 2004 and 2005, respectively, of which 5 and 3 units, respectively, failed delivering any data).

Accuracy of GLS loggers of the same model we used had been previously measured in trials with free-ranging albatrosses and yielded a mean error of 186 km (Phillips et al. 2004). The longitude estimate is generally more accurate than the latitude estimate (standard deviations of the mean in the albatross study were 110 and 185 km, respectively). One drawback of this method is an increased latitudinal error close to the periods of equinox, especially at the winter side. However, the longitude estimate is not affected. Fortunately the largely eastwards movement of our barnacle geese along a narrow coastal corridor facilitated reconstruction of shifts between stopover sites by relying on the longitude estimates alone. A more serious limitation for our study is that the GLS system requires at least a few hours of darkness to allow geographical fixes, hence measurements were not possible

after our birds crossed the Arctic Circle in late May. However, despite the limited accuracy and the need to retrieve units to download the records, GLS has advantages over other tracking techniques. The low weight and compact form of the unit that allow it to be attached to the leg ring keep any possible interference with the bird to a minimum. The energy consumption of the logger unit is very low, thus enabling a working duration over several years while providing, apart for the period around equinox, a high temporal resolution of fixes (i.e., two per day) the year round.

Tracking radio transmitters or PTTs (platform transmitter terminals) via satellite is now a widely used tool for studying animal movements. Timed fixes of high accuracy provide not only information about the migratory route, but also allow calculation of crucial migration parameters such as speed of migration and length of flying and resting bouts. These tantalising possibilities are subject to limitations, among them a possible impact on the animal's behaviour due to the weight or mode of attachment of the device. The safest way to minimise this potential interference is to avoid the use of any harness by implanting the device in the body cavity. This meant that only the transmitter's flexible antenna would protrude through the feathers. Inserting the transmitters while the geese were moulting gave the birds a few weeks to recuperate before taking to the wing again. By catching birds during the annual moult roundups and checking for rings we aimed to select individual females with a known breeding history. These individuals were then carried to our base camp where the transmitters were surgically implanted under anaesthesia under strict sterile conditions while monitoring heart rate (a twenty minute operation performed by A. Flagstad). The surgical implantation procedure followed the "abdominal implant technique" developed by Korschgen et al. (1996). Afterwards the implanted birds were returned to the catch area and released along with the others. There were no fatalities during this procedure. We used internal PTTs (built by Microwave, Maryland, USA) of 30 g (less than 1.5 percent of body mass of the migratory female goose). These devices were programmed to broadcast in two cycles: from implantation in August 2004 through early April 2005 at 4 hrs on 90 hrs off, then for 8 hrs on 20 hrs off until batteries ran out (in late June-mid July 2005) potentially providing coordinates 6 times a week. Given the limited battery life of about 750 hrs, this schedule would provide us with detailed information about the spring journey, which was our main priority. In all, we deployed 16 satellite transmitters to 15 females and 1 male in the 2004 breeding season. One unit suffered technical failure and two went 'off the air' during the autumn hunt before the geese left the Arctic. The remaining 13 satellite carriers successfully reached their wintering grounds and returned to the breeding grounds the following spring where direct observation in the field confirmed breeding in eight individuals in the colony of original capture. For another two birds we did not succeed in locating the nest but judging from the consistent locations from ARGOS we assume they nested. Data generated by the ARGOS system was further handled and analysed with a Satellite Tracking and Analysis Tool (STAT, Coyne and Godley 2005).

Route maps for three birds are illustrated in Figure BoxA.1. During the pre-migratory fattening period Goose Clara was found in the Dollard estuary at the

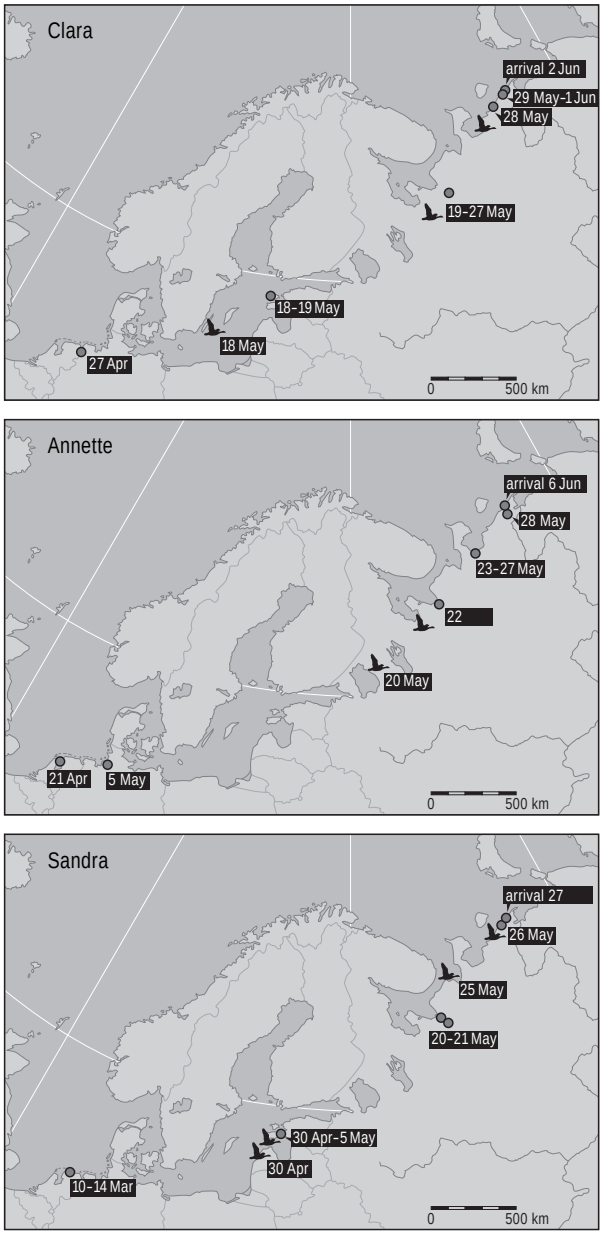

Figure Box A.1. Route maps of selected satellite-tagged birds (named Clara, Annette and Sandra) in spring 2005 (from Eichhorn 2005). Fixes from the same position (within a radius of 25 km) over several days are combined into one location marker. Bird silhouettes mark fixes during migratory flight. Note periods lacking position fixes in the western part of the study area. In this densely populated region the total emission of radio waves is high and may have hampered signal transmission of our PTTs to the satellite. The chance to be located by the satellite seemed greater during flight.

Dutch-German border, a staging site which has come in use only since the early 1990s. Clara left the North Sea on 18 May and reached the river Dvina near Arkhangelsk already the next day on 19 May, where she spent 8 days before heading to the breeding area. Except a pause of less than a day in western Estonia, this bird skipped Baltic staging sites altogether. In contrast, goose Sandra stayed in the Baltic at least since 30 April and probably until mass departure from there around 19 May. All three birds spent a relatively short time in the White Sea, likely influenced by an exceptionally early season in the breeding area (mean date of nest initiation was 7 June in 2005, compared to 12 June as the long-term mean). This allowed the birds to stay in close vicinity (< 100 km) of the colony already in the end of May, a time at which the area is in the grip of snow and ice in most other years.

Evaluating device-induced effects on survival

Attaching tracking devices to the geese was the only practical way for us to gather detailed knowledge of their long-distance migratory journeys. However, one should bear in mind the possible effects on the animal induced by these devices, not only for reasons of animal welfare, but also to assure the data obtained being representative for the animal under study, i.e., compared to unrestrained conditions. Information on the timing of migration and reproduction of tracked birds compared to birds without tracking devices is given in chapters 3 to 5 of this thesis (see also Eichhorn 2005). The following section examines whether survival of females equipped with these devices differed from control birds.

Methods

Apparent survival (Φ) and resighting probabilities (P) of adult female barnacle geese were estimated with Cormack–Jolly–Seber (CJS) capture–recapture models (Lebreton et al. 1992) in program MARK (White and Burnham 1999). Birds belonged to three different groups: 1) radiomarked with implanted Platform Transmitter Terminals (PTTs) and coloured legrings; 2) equipped with Global Location System (GLS) loggers and coloured legrings; 3) the control group: birds marked with inscribed coloured legrings only. Three of the 'PTT birds' received a GLS tag in addition and from one of these the tag was removed the next year. For the analysis here, requiring a reasonable sample size, we assigned these three birds to group 1. All females, regardless of group, were tagged in the breeding and moulting area at Kolokolkova Bay, Russia, when caught on the nest and/or during moult drives. Implantations of PTTs were conducted only during the moulting period. See above for details about devices.

Birds were resighted at two places and during two seasons per year from winter 2003 to summer 2006: 1) in the breeding and moulting area at Kolokolkova Bay, Russia during summer and 2) at their wintering grounds along the North Sea coast. The former resighting interval, referred to as 'summer', extended from June to August, the latter, defined as 'winter', lasted from December to February. Although

birds in the wintering area have been resighted also before and after this period, those observations are excluded in this analysis to restrict resighting intervals to a comparable length.

Thus the CJS models consisted of 3 groups (PTT, GLS, and ringed birds), 7 encounter periods (including initial captures) and spanned 3 years. However, in the PTT group the first 2 encounter periods (year 2003) contain no data because initial capture started in summer 2004. Furthermore, survival and recapture probabilities cannot be estimated separately in the final season (White and Burnham 1999). In cases where GLS loggers were removed from birds in the course of the study only encounter histories up to and including the moment of detachment were included in the analysis. An overview of numbers of geese and periods when gadgets/tags were deployed (removed) is given in Table Box A.1.

Table Box A.1. Year of capture and numbers of adult female barnacle geese marked with legrings only or receiving either a GLS tag or PTT implant in addition and used in the survival analysis.

Capture summer	PTT	GLS (removed)	Rings
2003		54	130
2004	15	6 (10)	60
2005		2 (5)	

Model selection was based on a modified Akaike's Information Criterion (AICc) (Anderson et al. 2000). Goodness of fit to the CJS model was tested using a bootstrap procedure provided in MARK. Using the bootstrap results, a scale parameter was calculated (č = 1.417) and used to adjust deviance and AICc values (QAICc). Starting with the full model containing main variable effects of group (g), season (s), years since capture (t), and all possible interactions among them, we first examined variation in resighting rate (P) while survival (Φ) was kept constant with the full design. P was constrained stepwise, beginning with the interaction terms followed by modelling of main effects. The resulting model with lowest QAICc was then used to model Φ following the same strategy. For the best candidate models for Φ derived from this exercise, additional constrains on P were tested to see if this might lead to models with even lower QAICc.

Results and discussion

Resighting probability was similar among years but differed between seasons (places) with a higher resighting probability on the breeding grounds (Table Box A.2, Fig. Box A.1). This pattern was enhanced for 'PTT birds' (causing an interaction between group and season) and birds from both groups equipped either with PTT or GLS tag were resighted at a higher rate than birds marked with coloured

Table Box A.2. Model selection for effects of group (g: PTT, GLS, and ringed birds), season (s) and time (t: years since capture) on survival (Φ) and resighting rate (P) of adult female barnacle geese from the Russian breeding site at Kolokolkova Bay. Models were ranked by the difference in the corrected Quasi Akaike's Information Criterion (Δ QAICc) relative to the model with lowest QAICc. Only the seven top models with Δ QAICc < 5.0 and the full model are presented.

No.	Model	Δ QAICc	Likelihood	Parameters	Deviance
1)	Φ(s), P(g*s)	0.000	1.000	8	164.4
2)	Φ(g*s), P(g*s)	1.852	0.396	12	158.0
3)	Φ(s), P(g+s)	2.555	0.279	6	171.0
4)	Φ(g+s), P(g*s)	2.592	0.274	10	162.8
5)	Φ(g+s+t,g*s), P(g*s)	3.714	0.156	14	155.7
6)	Φ(g+s+t), P(g*s)	4.473	0.107	12	160.6
7)	Φ(s), P(s)	4.508	0.105	4	177.0
	Φ(g*s*t), P(g*s*t)	25.338	0.000	29	145.5

legrings only (Fig. Box A.1). These differences are not surprising. First, the study birds are confined to a much smaller area during breeding and moult (i.e., the capture area) compared to the winter season spent along the North Sea coast. Second, prior to ringing the exact nesting site is generally not known and part of the ringed birds may come from colonies outside the study area. In contrast, most of the geese which received a GLS tag were caught on the nest and all of the 'PTT birds' had been previously marked and were seen nesting at a certain site. For these birds resighting probability is higher due to their faithfulness to a nesting territory.
The top model (no. 1) in Table Box A.2 does not indicate survival to be different among treatment groups, and the next best supported models that include a group effect (i.e., models 2 and 4) do not describe the data significantly better than the reduced model 1 (Likelihood Ratio Tests: $\chi^2 = 6.37$, df = 4, $P = 0.17$ and $\chi^2 = 1.51$, df = 2, $P = 0.47$, respectively). Survival estimates according to the top model (that is for birds from all groups combined) were 0.956 and 0.896 for survival from summer to winter and from winter to summer, respectively, yielding an annual survival of 0.856.

Most likely the same aspects causing a seasonal pattern in resighting probability are responsible for seasonal differences of survival (Fig. Box A.2). Survival from winter to summer is always lower for birds carrying legrings only since those likely include birds that are less likely to be seen in subsequent summers (ringed as non-breeders, stragglers). Survival from summer to winter is higher for these birds since in winter all birds have a similar chance to be seen regardless of their status (even if P is lower in absolute sense, Fig. Box A.1). To achieve more balanced resighting probabilities among groups for the summer it would be better to restrict the sample of birds from the group marked with rings only to those birds that were observed

breeding in the year of capture (i.e. seen with a nest). Essentially, this would require capture on the nest instead of captures during moult. Nevertheless, the aim of the present analysis was to test for group (treatment) effects and not to examine seasonal patterns of survival. The reason for choosing two resighting events per year was to run this preliminary survival analysis with data spanning over a period of only two to three years. With the extension of the study period to three and more years an analysis based on resightings restricted to the winter season will be possible in near future.

In conclusion, over the time of study (2-3 years since attachment of devices) we found no effects on the survival of geese potentially caused by the applied tracking tools. However, a re-examination at a later stage is advised to check for possible long-term effects. From the marked synchrony in timing of migration and breeding of birds with and without devices (ch. 3 and 4) we have great faith that the data obtained are representative for birds of our study population. Concerning the heavier PTT devices, studies on other waterfowl species confirm the notion that abdominally implanted devices compared to harness type attachments have least adverse effects on survival, breeding propensity and behaviour of the carrier (Garrettson and Rohwer 1998; Garrettson et al. 2000; Hupp et al. 2003; Hupp et al. 2006a).

Photo by René Adelerhof.

Chapter 2

Evaluation of the deuterium dilution method to estimate body composition in the barnacle goose: accuracy and minimum equilibration time

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Physiological and Biochemical Zoology (2008, in press)

Abstract

We examined body composition in barnacle geese (*Branta leucopsis*) by proximate carcass analysis and by deuterium isotope dilution. We studied the effect of isotope equilibration time on the accuracy of total body water (TBW) estimates and evaluated models to predict fat-free mass (FFM) and fat mass (FM) from different measurements varying in their level of invasiveness.

Deuterium enrichment determined at 45, 90 and 180 min after isotope injection did not differ significantly. At all sampling intervals isotope dilution spaces (TBWd) consistently overestimated body water determined by carcass analysis (TBWc). However, variance in the deviation from actual TBW was higher at the 45 min sampling interval, whereas variability was the same at 90 min and 180 min, indicating that 90 min is sufficient time to allow for adequate equilibration. At 90 min equilibration time, deuterium isotope dilution overestimated TBWc by 7.1% ± 2.6% ($P < 0.001$, paired t-test, n = 20). This overestimate was consistent over the range of TBW studied and TBWc could thus be predicted from TBWd ($r^2 = 0.976$, $P < 0.001$).

Variation in TBWc and TBWd explained, respectively, 99% and 98% of the variation in FFM. FM could be predicted with a relative error of ca. 10% from TBW estimates in combination with body mass (BM). In contrast, BM and external body measurements allowed only poor prediction. Abdominal fat fresh mass was highly correlated to total FM and, if the carcass is available, allows simple means of fat prediction without the necessity to dissect the entire specimen.

Introduction

Somatic stores are a key factor in defining an animal's body condition, and much of the variation in survival and reproduction has been attributed to the optimisation of body reserves (Blem 1990; Carey 1996a; Houston et al. 2007). Because of the central importance of energy and nutrient storage, their assessment has become an increasingly important aspect in current research (Brown 1996; Stevenson and Woods 2006). Birds in particular face the energetic dilemma of high energy expenditure for activity and maintenance and limitations of storage abilities due to their aerial lifestyle (McNab 2002).

A variety of methods have been applied to assess fat mass (FM) and fat-free mass (FFM) in vivo and vitro (overviews in Blem 1990; Brown 1996; Gessaman 1999; Speakman 2001; Stevenson and Woods 2006). These methods differ in accuracy to measure the variable of interest and in the degree of invasiveness for the study animal. Although proximate body composition analysis is regarded as the most accurate method, and the standard against which all other methods are evaluated, it obviously represents the most invasive, i.e. lethal, avenue. Additionally, it is a labour- and time-intensive method. From such carcass analyses researchers have recognised that an animal's body water content represents a fairly stable proportion of the FFM because lipids are stored nearly free of water (Pace and Rathbun 1945; Odum et al. 1964; Ellis and Jehl 1991). While some animals can experience large changes in body mass and composition, particularly during extensive periods of fasting, the relative water content in the fat-free mass (H_2O_{FFM}) seems not significantly affected (Groscolas et al. 1991; Cherel et al. 1992). Consequently, estimating total body water (TBW) content enables prediction of FFM and subsequently, in combination with total body mass (BM), FM. Indeed, many studies used body water content estimates to successfully predict body stores (Campbell and Leatherland 1980; Miller 1989; overview table VI in Blem 1990; Boos et al. 2000; but see Jamieson et al. 2006). Using calibrated regressions with dissectible fat depots, like abdominal and leg fat pads, represents another method to estimate total FM in carcasses without the necessity to analyse the entire specimen (Thomas et al. 1983; Piersma 1984; Boos et al. 2000; Jamieson et al. 2006).

The refinement of isotope analysis techniques has yielded non-destructive means to estimate TBW by the principle of isotope dilution, allowing longitudinal studies and work where killing the animal is not an option. This method relies on releasing isotopically labelled water molecules into the body water pool and after mixing determining isotope concentrations in body fluids (usually blood) of a single timed sample ('plateau approach') or a series of samples ('intercept approach') to derive an estimate of TBW (Speakman et al. 2001). Because it involves only one sampling event and a shorter experimental period the 'plateau approach' is less invasive for the animal. Additionally, a single sample reduces costs for material and analysis. However, using the 'plateau approach' appropriate timing of the single sample is important, i.e. after mixing of the marker with the body water is completed and before washout of the marker becomes effective. To reduce the latter,

captive animals are deprived of food and water during the equilibrium period. The time a wild animal is held in captivity can crucially affect its performance, in particular during the breeding period when parental care for a clutch or brood has to be provided. Our general research goal is to employ isotope dilution to assess body composition of incubating barnacle geese (*Branta leucopsis*) in the field. To this end, we want to reduce the equilibrium time without affecting data quality. Furthermore, it is known that the isotope-dilution method generally overestimates the actual TBW volume, because part of the labelled atoms exchange with non-aqueous body constituents (Culebras and Moore 1977; Schoeller et al. 1980). A review of studies employing hydrogen isotopes in four bird species revealed a considerable variation by which the dilution space differed from actual TBW ranging from underestimates of 2.3% to overestimates of 18% (Table 3 in Speakman et al. 2001). As has been noted frequently (Gessaman 1999; Shaffer et al. 2006; Mata et al. 2006) there is clearly a need for more bird studies evaluating estimates of TBW and other body components measured by isotope dilution against standard proximate body composition analysis.

In the present study on captive barnacle geese, we compared estimates of TBW, FFM and FM measured by proximate carcass analysis and by deuterium isotope dilution. Our specific objectives were to: (1) assess how equilibration time may compromise accuracy of the dilution method; (2) determine the level of overestimation of TBW by deuterium dilution; (3) evaluate the accuracy of predictions of FFM and FM from TBW and/or other predictor variables (BM, external morphological measurements, abdominal fat) depending on lethal and non-lethal approaches.

Methods

Animals and experimental setup

Animals were taken from a stock of barnacle geese kept at the Biological Centre of the University of Groningen in Haren, The Netherlands. Geese were kept on grassland while receiving *ad libitum* supplementary food (a mixture of grain and pellets). A total of 21 adult birds (≥ 2 years old), consisting of 10 females and 11 males, were selected to achieve maximal range in body condition; the body condition criterion was residual body mass from a regression of body mass on the first principal component from a factor analysis including tarsus and total head length. To further increase the variation in body condition a sub-sample of 2 females and 2 males were kept separately from the stock on grassland of lower food quality and with only limited supplementary food for 2 weeks prior to the experiment. Their average mass loss during this period was 210 ± 72.5 SD g. All animals were used in the carcass analysis, but only 10 of the 11 males for the isotope dilution space measurements, because of leakage of the isotope mixture through the puncture hole of the thin skin in 1 male. Birds were sexed by cloacal inspection and confirmed by examination of gonads during dissection. Most birds (16) were collected February to mid March 2006, the others (4 males, 1 female) on 21 April 2005.

To standardise treatment, animals were put in bird cages with no access to food but access to drinking water on the evening before the isotope-dilution experiment. The next morning (ca. 15 hours later), 2 hours before administration of the isotope solution, drinking water was removed until the end of the experiment, 4–6 hours later. The birds were intraperitoneal injected with a 99.9% deuterium isotope solution (Sigma Chemicals) using 1.0 ml insulin syringes. The actual mass of each volume injected was determined by weighing the syringe before and after injection on an analytical balance (Mettler AG204) to the nearest 0.1 mg. Average dose mass was 1.1153 ± 0.0021 SD g (n = 20). Blood samples were collected from 9 females and 7 males at each of the following sampling times: 45, 90 and 180 min after injection. Additionally, 1 female bird and 3 males were sampled at 90 min. To estimate deuterium background levels, blood samples prior to isotope administration were taken from 3 female and 3 male birds. Blood was collected from the brachial and intertarsal veins and stored in flame sealed micro-capillaries. After the last blood sample was taken, birds were fully anesthetized with 3 ml intraperitoneal injected Nembutal (natriumpentobarbital 60 mg/ml), followed by cervical dislocation 10–15 min later. Body mass was then measured to the nearest 1 g and carcasses were placed in plastic bags and refrigerated until being further processed next day or double-packed and frozen at –20°C until dissection and body composition analysis.

Daily care and management of the animals, as well as the experimental protocol was approved by the animal experimentation committee of the University of Groningen, license DEC 4081B.

Isotope analyses

The blood in the capillary tube was distilled in a vacuum line where water vapor was cryogenically trapped in a quartz tube using liquid nitrogen. After complete transfer, the vacuum system was brought to room pressure by admitting dry nitrogen. The insert was then quickly brought into a standard vial for automatic injection and sealed with a septum. During the sample preparation, internal water standards (gravimetrically prepared from pure deuterated water and also stored in flame-sealed capillaries) covering the entire enrichment range of the blood samples were distilled alongside the samples. This way, possible systematic effects on isotope enrichment due to the distillation process were accounted for. Such effects were also monitored in every batch by comparing the distilled standard waters with the same waters that were introduced into the vials directly. The actual δ^2H measurements were performed in automatic batches using a Hekatech High Temperature Pyrolysis unit (Gehre et al. 2004) in which the injected water reacted with the glassy carbon available in the reactor according to: $H_2O + C \rightarrow H_2 + CO$. The H_2 and CO gas, emerging into a continuous He flow through the system, were then led through a GC column to separate the two gases in time, and fed into a GVI Isoprime Isotope Ratio Mass Spectrometer for the actual isotope analysis. For the analysis of δ^2H (from the H_2 gas emerging first from the GC column) every sample was injected typically 6 times from the same vial into the furnace in 0.2 μl quantities. Memory effects of the HTP oven were corrected for using a memory correction

algorithm similar to the one described by Olsen et al. (2006). In the complete analysis scheme, several quality checks were incorporated. The isotope scales were calibrated using multiple distilled samples of two of the standard waters (being at the lower and higher end of the sample range, respectively), whereas the measured δ^2H values for a third standard, representing the expected midrange of blood samples, were used as quality "target" and had to be measured within 1% of its assigned values in order to meet the quality criterion for the batch. All sample analyses were run at least in duplicate, more times if values differed by more than 2.5%, and we used the average of values differing from each other by less than 2.5%.

Measurement of the hydrogen dilution space (TBWd)

Using the plateau approach (Speakman 1997) and employing equation (1) the hydrogen dilution space (TBWd) was calculated by taking into account the quantity of the dose (Q_d, mol), the ^2H concentration of the dose (C_d, atom %), the ^2H background concentration (C_b, atom %), and the ^2H concentration of individual blood samples (C_i, atom %) taken at the various sampling intervals.

$$TBWd = 18.02 \cdot Q_d \cdot (C_d – C_i) / (C_i – C_b) \quad \text{(Eqn. 1)}$$

Background levels of δ^2H measured in six birds prior to dose administration averaged 4.11‰ with a range of 33.01‰, which represented only 0.60% of the average measured deuterium enrichment after dose injection (5532‰, n=52). Therefore, we applied this average background value for all birds.

Dissection and body composition analysis

Fresh or thawed carcasses were weighed, all feathers plucked and re-weighed, the difference being plumage fresh mass. All skin was removed together with associated subcutaneous fat. The following organs were dissected out, weighed and analysed for water and fat content: left flight muscle complex (*pectoralis* and *supracoracoideus*), left leg musculature (attached to the *tibiotarsus* and *femur*), abdominal fat (a discrete deposit in the abdominal cavity, excluding mesenteric fat adhering to the intestines), gizzard, intestines (incl. mesenteric fat and *caeca*), heart, liver, spleen and kidneys. Prior to analysis the oesophagus, gizzard and intestines were emptied and reweighed. The total wet content excised from these organs was 20 ± 9 SD g. The right flight and right leg musculature were excised and retained for other work and their contributions to dry and fat free masses were estimated via the equivalent masses of their left counterparts. Organs were cut into small pieces of ca. 1 cm^3 and bones of the skeleton were broken to expose marrow and brain before oven-dried at 60°C until constant mass (7–15 days). Total body water from the carcass analyses (TBWc) was calculated as the carcass fresh mass after plucking minus the sum of all dried tissues, thereby accounting for general water loss during dissection. Thus water absorbed by feathers is intentionally not included in TBWc because it is not part of the body water pool into the isotope marker can be diluted. Lipids were

extracted from the tissues with a soxhlet apparatus using petroleum ether as solvent. We refer to whole body fat-free mass (FFM) as total wet lean mass, including feathers and skeleton, calculated from fresh body mass (BM) minus extractable fat mass (FM).

Calculations and statistics

Statistical analyses were performed with SPSS 14. All results are reported as mean ± 1 SD, unless stated otherwise, and were considered to be significant at $P < 0.05$. For all parametric tests assumption of normality and homogeneity of variances were evaluated using the Kolmogorov-Smirnov test and Levene's test, respectively (Zar 1999). As a measure of structural size we derived scores of the first principal component (PC1) from a factor analyses based on four external measurements: the length of tarsus, total head (i.e., including bill), maximum wing chord and keel (measured from the anterior tip of the *carina* to the end of the *sternum*, at the transition with the abdominal cavity). Tarsus was measured with callipers to the nearest 0.1 mm; all other variables were measured with a ruler at 1 mm accuracy. Variables had a similar factor loading (0.72 - 0.94) on PC1, which explained 73% of the total variance. We used ANOVA to test for mean differences among sex, and GLM, with PC1 included as covariate.

Differences in estimated dilution space with time after isotope injection were compared by a repeated measure ANOVA. Two-tailed paired t-tests were used to compare means of isotope dilution space (TBWd) and body water based on carcass analysis (TBWc). We used estimated TBW and other predictor variables (see below) to predict FM and FFM by two approaches: (A) multiple regression analyses and (B) assuming a constant FFM hydration.

A) We applied a stepwise backward elimination procedure in the multiple regression analyses. Starting with the non-destructively obtained variables tarsus, head, wing, keel, BM and sex as basic model, we extended the set of predictor variables and included either TBWd and dry BM or TBWc and dry BM to investigate if FM predictions could be improved. Finally, we took the set of predictor variables from the basic model and included additionally abdominal fat fresh mass (i.e., of the dissected fat pad, not chemically extracted fat). Before we included abdominal fat in multiple regressions, we tested if a curvilinear relationship between FM and abdominal fat would be more appropriate than a linear fit (Piersma 1984). Although the coefficient of determination increased slightly from $r^2 = 0.90$ to $r^2 = 0.92$, adding a quadratic term did not significantly improve a linear fit of FM to abdominal fat ($P = 0.06$).

We used double cross-validation to evaluate the robustness and replicability of regression equations following the procedure described by Guan et al. (2004). Briefly, subjects from the original data set were randomly assigned to two groups, equal or similar in number and sex-ratio of subjects. The statistically significant predictor variables derived from the original full data set were applied in both subgroups to develop predictive equations and derive coefficients of determination (r_{11}^2 and r_{22}^2; first subscript number refers to subsample's data and second

subscript number to subsample's regression coefficients). Standardised regression coefficients and Z scores of predictor variables and of the response variable were used in all cross-validation procedures. The predictors' regression coefficients were crossed over the two subsamples to produce equations and coefficients of determination (r_{12}^2 and r_{21}^2) from actual group data using the regression coefficients from the other group for the predictions. Using this double cross procedure two shrinkage values were calculated: $r_{11}^2 - r_{12}^2$ and $r_{22}^2 - r_{21}^2$. The more closely the shrinkage estimate approaches zero, the greater the degree of stability across subsamples. Furthermore, two invariance coefficients were derived by correlating the predicted values of subsample 1 with the predicted values of subsample 1 using the regression coefficients of subsample 2 (r_{11-12}) and *vice versa* (r_{22-21}). As these invariance coefficients approach one, more confidence can be obtained in the replicability of the results.

B) As alternative to calibrated regression equations and assuming a constant water content in the FFM (H_2O_{FFM} = TBW:FFM = constant) the individual FFM and FM can be inferred from following equations:

$$FFM = \frac{TBW}{H_2O_{FFM}} \quad \text{(Eqn. 2)}$$

$$FM = BM - FFM \quad \text{(Eqn. 3)}$$

We will refer to this approach as the Pace and Rathbun (1945) approach (*sensu* Mata et al. 2006).

Results

Body composition by carcass analysis

Carcass analyses are listed in Table 2.1. Animals in this study covered a broad scale of body mass and composition, ranging twofold in body mass and from 2% to 25% in lipid content. Males were larger than females according to PC1, the first principal component from a factor analysis including tarsus, wing, skull and keel length ($F_{1,19} = 31.18$, $P < 0.001$). Significant differences between sexes were also found for body mass, TBW and FFM. However, these were caused by the sex-related differences in structural size. Thus, when sex was tested together with PC1 in one analysis to explain differences in BM, TBW and FFM, only PC1 explained a significant part ($P < 0.05$ in all models) whereas variation due to sex became non-significant. Females in our sample tended to have higher fat loads (FM:BM, $F_{1,19} = 3.39$, $P = 0.08$).

TBW measured by deuterium dilution and the effect of equilibration time

Within-individual variation in deuterium isotope enrichment occurred mainly between the first two sampling events and was independent of the size of the indi-

Table 2.1. Whole body composition by carcass analysis. Given are body mass (BM), total body water (TBWc), fat-free mass (FFM), fat mass (FM) and fractions (%) of water and fat content for sexes combined and males and females separately.

	Total	Males		Females	
	n=21	n=11	Range	n=10	Range
BM (g)	1,995 ± 241*	2,104 ± 183	1,893-2,515	1,876 ± 248	1,479-2,185
TBWc (g)	1,121 ± 152*	1,213 ± 112	1,079-1,457	1,020 ± 125	799-1,209
FFM (g)	1,773 ± 224*	1,907 ± 159	1,729-2,273	1,625 ± 193	1,263-1,901
FM (g)	222.5 ± 110.7	196.4 ± 99.0	37.1-330.6	251.2 ± 120.9	95.6-539.6
TBWc:BM (%)	56.2 ± 3.9 [a]	57.7 ± 3.7	52.9-62.9	54.6 ± 3.5	46.9-59.3
TBWc:FFM (%)	63.2 ± 1.1 [a]	63.5 ± 1.3	61.8-65.4	62.8 ± .8	61.1-63.8
FM:BM (%)	11.1 ± 5.1	9.2 ± 4.5	2.0-15.3	13.1 ± 5.2	6.5-24.7

* Significant differences between sexes ($P < 0.05$). [a] Including fresh plumage mass in BM; if plumage is excluded from BM, the fractions are TBWc:BM = 60.6 ± 4.1% and TBWc:FFM = 68.8 ± .8%.

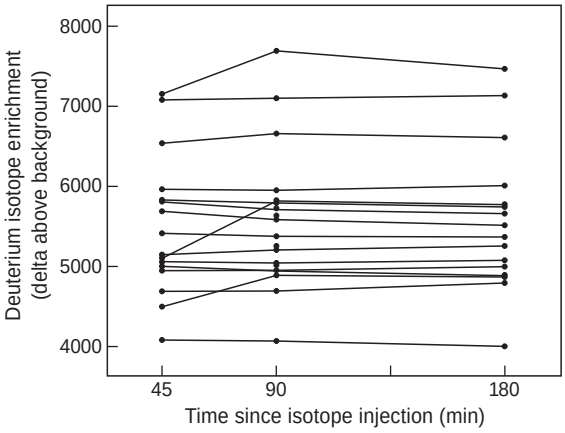


Figure 2.1. Deuterium isotope enrichment determined for 16 animals sampled at 45 min, 90 min and 180 min after isotope injection plus another 4 animals sampled at 90 min after dose administration.

vidual body water pool (Figure 2.1). However, a pronounced increase over this period was restricted to a few individuals only, and overall changes between sampling times were too low to be significant (repeated measures ANOVA, $F_{2,30} = 1.894$, $P = 0.168$).

At all sampling intervals carcass body water was significantly overestimated by the deuterium dilution space ($P < 0.001$, paired *t*-test), ranging from average values of 9.2% at 45 min to 7.1% at 90 min (Table 2.2). This overestimate was consistent over the range of TBWc studied ($P > 0.05$ for all regression models at the various

Table 2.2. Deuterium dilution space (TBWd) measured at different sampling intervals and in relation to total body water from carcass analysis (TBWc). Data present means ± SD. Further are given coefficients of determination (r^2) together with the standard errors of the estimates (SEE, i.e. the root mean square errors) from linear regressions of TBWc vs. TBWd ($P < 0.001$ for all regressions).

	45 min	90 min		180 min
	n=16	n=16	n=20*	n=16
TBWd (g)	1,198 ± 185	1,179 ± 187	1,190 ± 169	1,182 ± 185
TBWd:TBWc	1.092 ± .054	1.073 ± .027	1.071 ± .026	1.076 ± .024
$r^2_{TBWc–TBWd}$ (SEE in g)	.90 (51)	.98 (22)	.98 (23)	.98 (20)

* Includes four birds which were not measured at 45 and 180 min.

sampling times). The accuracy to predict TBW from deuterium dilution, was on average slightly better at 90 and 180 min than at 45 min but this difference was not significant (repeated measures ANOVA, $F_{2,30} = 2.130$, $P = 0.136$). Variance of the ratio of TBWd:TBWc was significantly different between sampling events (Levene test: $F_{2,49} = 4.473$, $P = 0.016$). The error in the deviation of TBWd from TBWc was twice as high at 45 min compared to 90 and 180 min after dose administration (Table 2.2) leading to a reduced precision of TBW predictions from isotope measurements at this early sampling stage. The following regression equations were derived to predict TBWc from TBWd:

at 90 min (n = 20): $TBWc = 96.034 + 0.852 \cdot TBWd$ (Eqn. 4)
at 180 min (n=16): $TBWc = 94.544 + 0.848 \cdot TBWd.$ (Eqn. 5)

Further on, when using deuterium dilution space as predictor variable to estimate body composition, we employed TBWd values measured at 90 min.

Estimates of body composition by lethal and non-lethal methods

TBW determined either from carcass analysis or isotope dilution was a very strong single predictor for FFM explaining 98-99% of the variation in FFM (Figure 2.2). Table 2.3 compares the outcome of multiple regression analyses using TBW measured by deuterium isotope dilution and carcass analysis and further predictors related to different levels of invasiveness. The errors in the prediction of FM and FFM (calculated as deviations of predicted from observed values) following the Pace and Rathbun (1945) approach are also listed in Table 2.3. For the latter approach we applied individual estimates of TBW from the established relationship between TBWc and TBWd (measured at 90 min equilibrium time) and a H_2O_{FFM} of 63.2% (i.e., the average from our sample). We presented only predictive equations for FM because the absolute error of prediction was the same for FM and FFM, regardless if the one or other component was taken as response variable. This was due to same

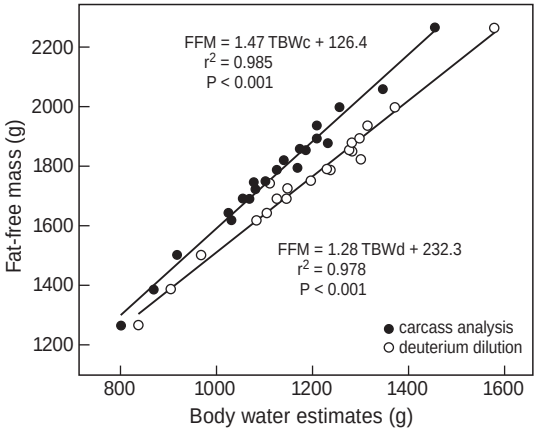


Figure 2.2. Relationships between fat-free mass and body water determined by carcass analysis (closed circles, n = 21) and deuterium dilution (open circles, n = 20).

significant predictors (model 1 to 3) for both FM and FFM and the fact that they add up exactly to BM. Thus FFM was calculated as FFM = BM – FM. Also, we were mainly interested in the variation of FM (the relatively smaller of both components) and to what extent it can be accounted for by the various regression models.

Much of the variation in FM was unaccounted for by model (1) based on body mass and external body measurements. Furthermore, relatively strong r^2 shrinkage and low invariance coefficients indicate lower replicability of the prediction when applied to different sub-samples compared to the other models. FM was not significantly related to any of the potential predictors offered to model (1) separately. Only the combination of BM and a structural measurement (keel) revealed a significant relationship with FM. The combined variables dry BM (i.e. BM – TBW) and TBW determined from isotope dilution (model 2) or carcass analysis (model 3) both explained a large part of the variation in FM (92% and 97%, respectively). Moreover, the results from a cross-validation showed good replicability of the respective equations. When dry BM was replaced by BM in models (2) and (3) errors of prediction and r^2 were the same. However, such alternative models suffered notably from multicollinearity of the predictors (see VIF in Table 2.3) making them less robust. Abdominal fat fresh mass was highly correlated to total FM and, if the single predictor in the model, accounted for 90% of the variation in FM. The variation increased slightly to 93% when head length was added to this model.

Table 2.3. Predictive equations for total fat mass (FM in g) based on non-lethal and lethal measurements in 21 barnacle geese (n=20 if TBWd is used in the equation). Modelling started with non-invasively measurable predictors in model no. 1: tarsus, head, wing, keel, BM and sex. This set of potential predictors was expanded by TBWd, dryBM (i.e. BM - TBWd) and TBWc, dryBM (i.e. BM - TBWc) in model no. 2 and 3, respectively. For model no. 4 the same predictors as for model 1 were applied with addition of abdominal fat fresh mass F_{abd}. Shown are the final models containing only significant predictor variables derived by stepwise backward multiple regressions. $P < 0.001$ for all models except no. 1, $P = 0.008$. Summary statistics include coefficients of determination (r^2), standard error of the estimate (SEE), absolute and relative error of predicted FM and FFM calculated as deviations of predicted from observed values (mean ± SD), variance inflation factors of predictors (VIF) and statistics from a cross-validation procedure (see methods for details). FFM was calculated as BM – FM (see also text). Outcomes of the Pace and Rathbun (1945) approach are given in the last row (n=20).

			Absolute error FM and FFM	Error FFM	Error FM	VIF	Shrinkage		Invariance coefficients	
	r^2	SEE	(g)	(%)	(%)		$r_{11}^2–r_{12}^2$	$r_{22}^2–r_{21}^2$	$r_{11–12}$	$r_{22–21}$
Multiple regression models										
Non-lethal										
1) FM = 368.7+ 0.329·BM - 6.997·Keel	0.418	89.1	69.9 ± 44.8	4.0 ± 2.8	37.3 ± 24.9	1.42	0.19	0.11	0.84	0.74
2) FM = -200.6 - 0.266·TBWd + 0.936·dryBM	0.918	33.7	21.3 ± 23.3	1.2 ± 1.4	10.1 ± 10.1	1.15[a]	0.02	0.01	0.99	0.99
Lethal										
3) FM = -57.48 - 0.418·TBWc + 0.856·dryBM	0.966	21.6	16.0 ± 12.3	0.9 ± 0.8	10.6 ± 11.4	1.18[b]	0.14	0.12	0.93	0.94
4) FM = -382.7 + 4.492·F_{abd} + 5.223·Head	0.931	30.1	24.9 ± 13.8	1.4 ± 0.8	16.0 ± 18.4	1.01	0.01	0.01	1.00	1.00
Pace and Rathbun (1945) approach			22.1 ± 26.0	1.3 ± 1.5	12.7 ± 17.1					

[a] When dryBM is replaced by BM in the model VIF = 4.51.
[b] When dryBM is replaced by BM in the model VIF = 3.68.

Discussion

We found a strong relationship between TBW measured by carcass desiccation and by deuterium isotope dilution in barnacle geese, which was consistent over a large range in body composition. With knowledge of this relationship and of the minimum equilibrium time needed for the isotope dose to mix completely with the body water pool, TBW can be very accurately predicted by deuterium isotope dilution as non-lethal method. Furthermore, an accurate estimate of TBW was a strong predictor of FFM and, in combination with BM, FM. However, the accuracy of the estimates of FFM and FM for additional samples on the basis of TBW measured isotopically or by desiccation largely depends on the variation of the relative water content in the FFM.

Body composition by carcass analysis
The dissected barnacle geese showed pronounced sexual differences in structural size and, related to this, differences in BM, FFM and TBW. Higher fat loads in females may be expected in geese, in particular during the pre-breeding phase, in anticipation of egg production and incubation (Raveling 1979).

Fat-free mass hydration in birds - how variable is it?
Whenever total body water, or an estimate thereof, is used to predict FFM, the variation of H_2O_{FFM} is of crucial relevance, because it comprises the other major error source, beside the error of the TBW estimate. Wang et al. (1999) reviewed this issue for adult mammals, and concluded that species share a relatively constant H_2O_{FFM}, in spite of differences in body mass ranging by a factor of 10^4. The relatively higher water content in the lean body component of the young growing organism until it reaches chemical maturity is well known (e.g., Arnould et al. 1996 for mammals; Bech and Østnes 1999 for birds), and thus we will restrict ourselves to mature birds in the following discussion.

When comparing results of H_2O_{FFM} among studies first of all attention has to be paid to possible differences in methodologies and definitions applied in these studies. Researchers often include water adsorbed to the feathers in the amount of TBW, which may amount to ca. 1-2.5% of TBW (Crum et al. 1985; Mata et al. 2006). We intentionally did not so because this 'external water' is not in exchange with the body water pool estimated by isotope dilution (Crum et al. 1985). Further, FFM may be differently defined among studies, excluding, for instance, plumage (e.g., Boos et al. 2000; Mata et al. 2006) or bones and plumage (e.g., Groscolas et al. 1991) from the FFM component. Consequently, estimates of H_2O_{FFM} from those studies (71% – 73%) are necessarily considerable higher than the value reported here.

In Table 2.4 we compiled data on H_2O_{FFM} reported or calculated from studies of waterfowl carcass analyses using comparable methods and definitions as applied in the present study. H_2O_{FFM} can be reasonably stable over different seasonal and/or physiological stages within a given study. As in our study no sex-related differences are indicated. Variation between studies can be, however, considerable.

Table 2.4. Data on H_2O_{FFM} in adult waterfowl. In most cases H_2O_{FFM} was calculated from mean values of BM, FM and TBW (except: from individual values in Korte (1988); Campbell and Leatherland (1980) gave mean values directly). We used only samples (means) where the same birds were analysed for all of those body components; n=sample size, se=standard error.

species / source	period of collection	H2OFFM (%)			
Lesser Snow Goose (*Anser c. caerulescens*) (Campbell and Leatherland 1980)	through the year	69.3 (se=0.06)[a] (sexes pooled)			
		Females	n	Males	n
Barnacle Goose (this study)	winter - spring	62.8 (se=0.2)	10	63.5 (se=0.4)	11
Brent Goose (*Branta bernicla*) (Korte 1988)	winter - spring	69.0 (se=0.6)	14	68.4 (se=0.5)	21
Canada Goose	autumn migration	65.2	6	63.5	9
(*Branta canadensis*)	midwinter	62.6	5	62.9	10
(Raveling 1979)	spring migration	65.7	11	65.8	5
	pre-lay	63.4	4	65.4	5
	mid-incubation	65.4	2	66.5	1
	hatch day	66.1	9	65.2	6
	early moult	68.7	8	68.1	9
	mid-moult	67.5	2		
	mean	65.6		65.3	
Common Eider	2-3 weeks pre-lay	63.6	4		
(*Somateria mollissima*)	pre-lay breeders	64.4	7		
(Parker and Holm 1990)	pre-lay non-breeders	66.5	2		
	post-lay	63.9	7		
	hatch day	64.6	8		
	mean	64.6			
Black Duck	pre-lay	64.5	4		
(*Anas rubripes*)	laying	64.3	12		
(Reinecke et al. 1982)	post-lay	65.0	16		
	moult	63.8	3		
	autumn	63.2	7		
	winter	60.3	11		
	mean	63.5			
Lesser Scaup	pre-moult	73.3	21		
(*Aythya affinis*)	moult	70.8	24		
(Austin and)	post-moult	71.5	8		
Fredrickson 1987	migratory	70.8	32		
	mean	71.6			
All studies	mean	66.6 (se=1.2)[b]	7		

[a] TBW component included water adsorbed to feathers. Source was unclear about the actual sample size related to the reported mean and standard error of 0.693 ± 0.06. Translated into % this standard error would equal a questionable se = 0.0006%. We suspect 0.06 being the correct value.

[b] Mean of studies' means; for studies where data for both sexes were available the average was used.

Compared to other studies our values (mean = 63.2%) are at the lower range of H_2O_{FFM} values reported so far. Although the geese had access to water during the captive period until 4-6 hours before termination of the experiment, due to general capture stress they may have not made sufficient use of it and experienced a certain degree of dehydration. Birds can tolerate notable water losses under restrained conditions. For instance, Davidson (1984) noted a decrease of H_2O_{FFM} of 0.8-1% per hour over the first four hours after capture in knots (*Calidris canutus*) and dunlins (*C. alpina*), i.e. from 66.7% to 63.5% and from 65.8% to 61.8%, respectively. Interestingly, after the first 4 hours Dunlins appeared to fully compensate further water loss by metabolically produced water, whereas in knots dehydration continued (at lower rate) until 60.9% at 24 h after capture.

We conclude that both methodological factors and tolerance for a (temporarily) negative water balance in birds may contribute to the considerable variation in H_2O_{FFM} reported among studies. Nevertheless, homeostasis is crucial for organismal functioning. Therefore, under unrestrained circumstances birds will probably strive to avoid dehydration and keep their water balance within small margins. Currently, it is not possible to rule out if and to what extent variation in H_2O_{FFM} reflects truly species-specific diversity or varying sampling procedures and other methodological differences. Future applications of the isotope dilution method to estimate body composition would benefit from a better understanding of general patterns of variation in H_2O_{FFM} and how it maybe related to species and/or physiological state.

TBW measured by deuterium dilution and the effect of equilibration time

In the present study TBWd overestimated TBWc by 7.1% (at 90 min equilibrium time) consistently over a large range of TBWc; and can thus be corrected according to the values given here. Speakman et al. (2001, Table 3) calculated an average of 4.7% by which actual TBW was overestimated by hydrogen isotope dilution in birds, based on nine studies on four species. Additional studies using hydrogen isotopes together with the 'plateau approach' reported 8.1% for the chicken *Gallus gallus* (Mata et al. 2006), 8.4% for glaucous-winged gull *Larus glaucescens* nestlings (Hughes et al. 1987) and 3.3% for the glaucous gull *Larus hyperboreus* (Shaffer et al. 2006). However, at least part of the variation among studies is due to methodological factors. For instance, the study of Degen et al. (1981), which was included in the average calculated by Speakman et al. (2001), as well as Hughes et al. (1987) and Shaffer et al. (2006) included water adsorbed to feathers in TBWc. This plumage water cannot be accounted for by isotope dilution. As a consequence, the difference of TBWd to TBWc becomes smaller. Thus, an average value by which carcass TBW is overestimated by the hydrogen dilution space in birds certainly exceeds the 4.7% given by Speakman et al. (2001).

Our results indicate that mixing of marker solution and body water was not completed after 45 min. Average levels and variability were the same at 180 min and 90 min, indicating that 90 min is sufficient time to allow for adequate equilibration. Apparently, compared to an earlier estimate of about 4 hours for this

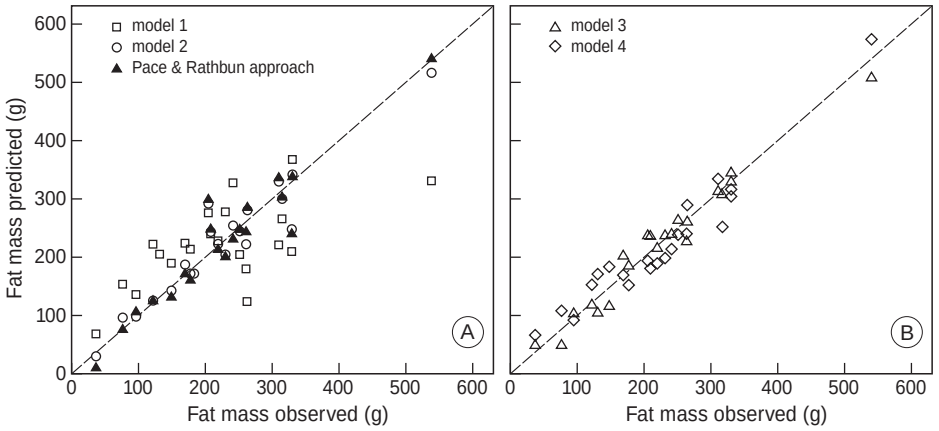


Figure 2.3. Relationships between fat mass determined by carcass analysis and predictions of models presented in Table 2.3. Panel (A) refers to non-lethal methods, panel (B) to lethal methods. The dashed line represents a relationship of Y=X.

species (Nolet et al. 1992) equilibration time can be considerably reduced without compromising accuracy of the TBW estimate, thereby reducing disturbance to the animal.

Estimates of body composition by lethal and non-lethal methods

Regression models to predict body composition based on BM in combination with other external morphological parameters performed poorly in the present study on the barnacle goose (Table 2.3 and Figure 2.3). BM alone was unable to explain a significant part in FM variation. In contrast Skagen et al. (1993) found in two sandpiper species 76% and 89% of the variance in FM explained by BM. There are two main reasons why BM alone may be a weak predictor for FM. First, changes in BM can involve, beside fat, appreciable amounts of protein, and the relative contribution of both components may vary over periods of mass change. Studies on geese provided good examples (Newton 1977; Raveling 1979; Prop and Spaans 2004) where such changes were related to seasonal and physiological stages like migration, reproduction and moult. Second, study subjects usually differ in structural size and such differences are generally unrelated to lipid contents, although some relationship may occur when fat is deposited in the bone marrow, which can reach significant levels in waterfowl (Hutchinson and Owen 1984). Additional incorporation of structural measurements can improve the predictive power of the model but does account for only part of the overall structural size differences. Because FFM includes virtually all structural mass and, at the same time, nearly all water, a measure of TBW accounts much better for differences due to structural mass than most morphological measurements. Indeed, variation in TBW determined from carcass analysis or isotope dilution both explained a large part of the variation in FFM and, consequently, in FM.

Abdominal fat fresh mass was highly correlated to total FM and, if the carcass is available, allows simple means of fat prediction without the necessity to dissect the entire specimen. Model (1) represented the least invasive of the methods tested in Table 2.3. However, the error of prediction was highest, equating to 37% and 4.0% of actual FM and FFM, respectively. Using estimates of TBW from deuterium isotope dilution and either a regression or Pace and Rathbun (1945) approach as alternative non-destructive methods reduced the relative error of the FM and FFM estimate to 10 – 13% and 1.2 – 1.3%, respectively.

Differences in accuracy of the regression and the Pace and Rathbun (1945) approach depend on how much individual animals in the study sample deviate from the assumption of a constant FFM hydration. Variation in H_2O_{FFM} was low in our sample (Table 2.1) resulting in a similar accuracy of both approaches (Table 2.3 and Figure 2.3). Irrespective of which approach is applied, prediction accuracy for a new sample will be reduced if H_2O_{FFM} differs between calibration sample and new sample. A direct measurement of H_2O_{FFM} in a sub-sample of the study population is always advisable to ensure confidence about resulting predictions. If this is not possible, we suggest to apply an average value of 66.6% for studies on adult waterfowl, as calculated from the species-specific studies listed in table 2.4, when using the Pace and Rathbun (1945) approach.

Acknowledgements

We want to thank Astrid Tijdens and René Adelerhof for their assistance in experimental work and carcass analysis. Berthe Verstappen-Dumoulin determined the ^2H enrichments and Harro Meijer provided a description of the isotope analysis procedure. Marcel Klaassen, Sarah Jamieson, Joost Tinbergen and Rudi Drent are thanked for their valuable comments on earlier versions of the manuscript. GE was supported by scholarships from the 'Marianne und Dr. Fritz Walter-Fischer Stiftung', Germany, and the 'Ubbo Emmius Programme' at the University of Groningen.

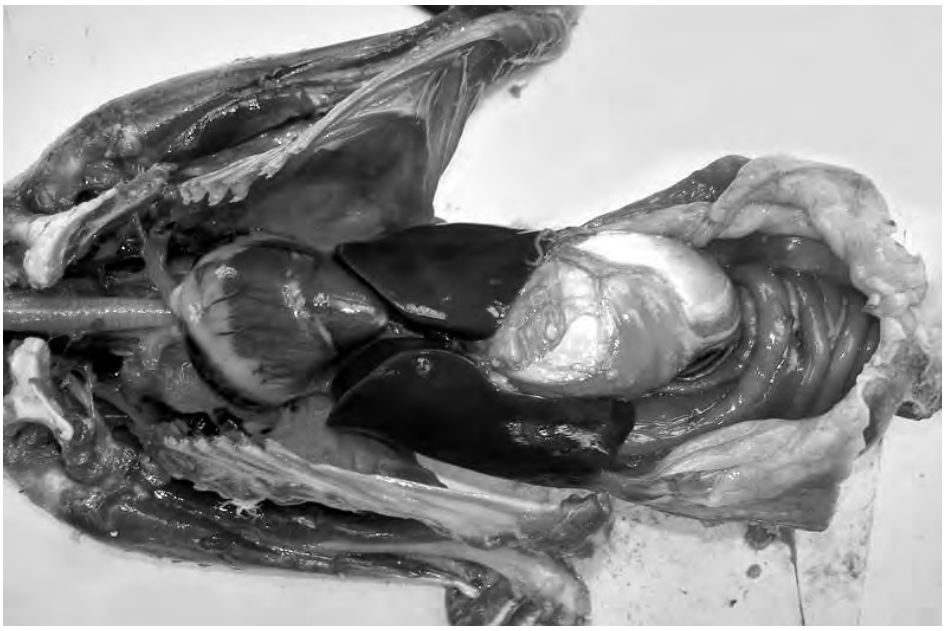


Photo by René Adelerhof.

Box

B

Organ composition of barnacle geese

Götz Eichhorn
Astrid Tijdens
René Adelerhof

In chapter 2 we presented results of total body composition of 21 barnacle geese *Branta leucopsis* (10 females, 11 males) performed as part of an evaluation of the deuterium dilution method. Making use of the same sample of birds, we here present details on the composition of certain tissues and on length measurements of parts of the digestive tract.

Methods

Animals were taken from a stock of barnacle geese kept at the Biological Centre of the University of Groningen in Haren, The Netherlands. The flightless birds (wing feathers of one wing clipped) were kept on grassland while receiving *ad libitum* supplementary food (a mixture of grain and pellets). Birds were fully anesthetized with 3 ml intraperitoneal injected Nembutal (natriumpentobarbital 60 mg/ml), followed by cervical dislocation 10–15 min later. Body mass was then measured to the nearest 1 g and carcasses were placed in plastic bags and refrigerated until being further processed next day or double-packed and frozen at -20ºC until dissection and body composition analysis. After feathers were plucked from the whole body all skin was removed together with associated subcutaneous fat. Following organs were dissected out, weighed and analysed for water and fat content: left and right flight muscle complex (*M. pectoralis* and *supracoracoideus*), leg musculature (attached to the *tibiotarsus* and *femur*), abdominal fat (a discrete deposit in the abdominal cavity, excl. mesenteric fat adhering to the intestines), gizzard, intestines (incl. mesenteric fat and *caeca*), heart, liver, spleen and kidneys. The remainder was named "rest". Length of the oesophagus (cut at the base of the tongue and incl. the *proventriculus*), intestines (cut at the gizzard) and caeca (left and right separate) were measured to the nearest 1 mm. Oesophagus, gizzard and intestines were emptied before the analysis, and the oesophagus was added to the "rest". The excised right flight and right leg musculature were retained for further study and therefore their contributions to dry and fat free masses were estimated via the equivalent masses of their left counterparts. Organs were cut into small pieces of c.

Table Box B.1. Fresh mass, water content, water content in the fat-free mass H_2O_{FFM} and fat content of dissected tissues, and length measurements of parts of the digestive tract.

Tissue	Mass (g)	H_2O (%)	H_2O_{FFM} (%)	Fat (%)	n
Skin	205.6 ± 61.7	32.0 ± 11.6*	57.7 ± 5.9	44.4 ± 18.9	21
Flight muscles	461.8 ± 77.5	71.2 ± 0.7	72.8 ± 0.5	2.2 ± 0.7	21
Leg muscles	210.0 ± 34.5*	71.0 ± 2.4	76.0 ± 3.4	6.4 ± 4.5	21
Abdominal fat	36.2 ± 23.0	14.4 ± 8.3	80.0 ± 8.9	82.4 ± 9.3	20[a]
Heart	19.5 ± 2.9*	70.7 ± 3.1	77.9 ± 1.1	9.3 ± 3.4	21
Liver	33.9 ± 8.4	72.1 ± 2.8	74.6 ± 2.6	3.3 ± 3.9	21
Spleen	1.5 ± 1.5	72.5 ± 4.0	74.2 ± 5.1	2.2 ± 4.2	17[b]
Intestines	45.9 ± 12.9	57.2 ± 10.1	75.5 ± 7.2	24.2 ± 11.2	21
Gizzard	46.0 ± 7.0	71.1 ± 2.3	76.2 ± 2.1	6.7 ± 2.9	21
Kidneys	9.9 ± 2.1	70.8 ± 5.2	77.2 ± 2.1	8.3 ± 6.4	21
Rest	783.3 ± 109.7*	60.3 ± 2.4	64.7 ± 1.4	6.9 ± 2.3	21
Plumage	143.7 ± 16.5				21

	Length (mm)	n
Oesophagus	307.4 ± 48.0	20[c]
Intestines	1,415 ± 176.3	21
Left caeca	217.2 ± 29.1	21
Right caeca	216.2 ± 30.7	21

* Significant differences between sexes ($P < 0.05$): fresh mass (g) of Leg muscles, Heart and Rest was 227.5 ± 28.3, 20.9 ± 2.6 and 863.4 ± 72.1 for males and 190.7 ± 31.1, 18.0 ± 2.4 and 695.2 ± 67.3 for females, respectively; Skin water content (%) was 37.0 ± 12.3 for males and 26.5 ± 8.1 for females.

[a] virtually no fat tissue present.

[b] three samples excluded because of unaccounted water loss or damage; one sample (outlier) showed unusual enlargement (23.3 g).

[c] one measurement missing.

1 cm^3 and bones of the skeleton were broken to expose marrow and brain before oven-dried at 60°C until constant mass (7–15 days). Care was taken to measure fresh weight of organs as soon as dissected, however, a certain water loss is inevitable and values of hydration should be regarded as minimum values. Fat extraction was done with a soxhlet apparatus using petroleum ether as solvent.

All results are reported as mean ± 1 SD and were considered to be significant at $P < 0.05$. Assumption of normality and homogeneity of variances were evaluated using the Kolmogorov-Smirnov test and Levene's test, respectively (Zar 1999). Pearson correlation coefficients were applied to evaluate relationships among tissue-specific and total fat loads. Statistical analyses were performed with SPSS 14.

Results and discussion

Whole body mass differed significantly between male and female barnacle geese due to sexual differences in structural size (ch. 2). At tissue level, fresh masses of

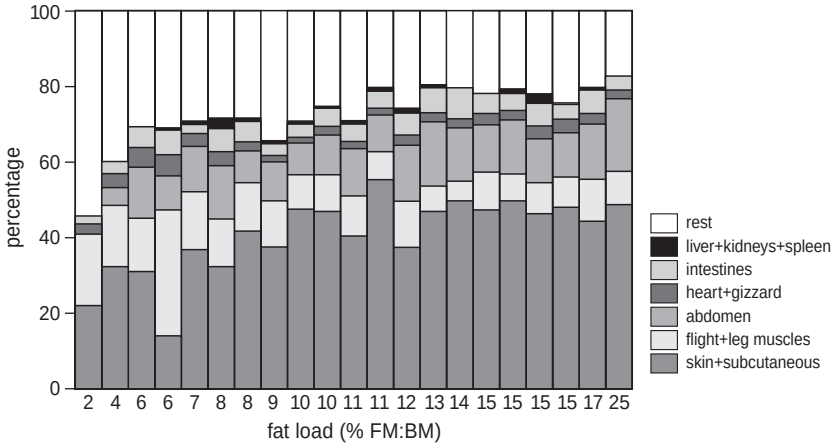
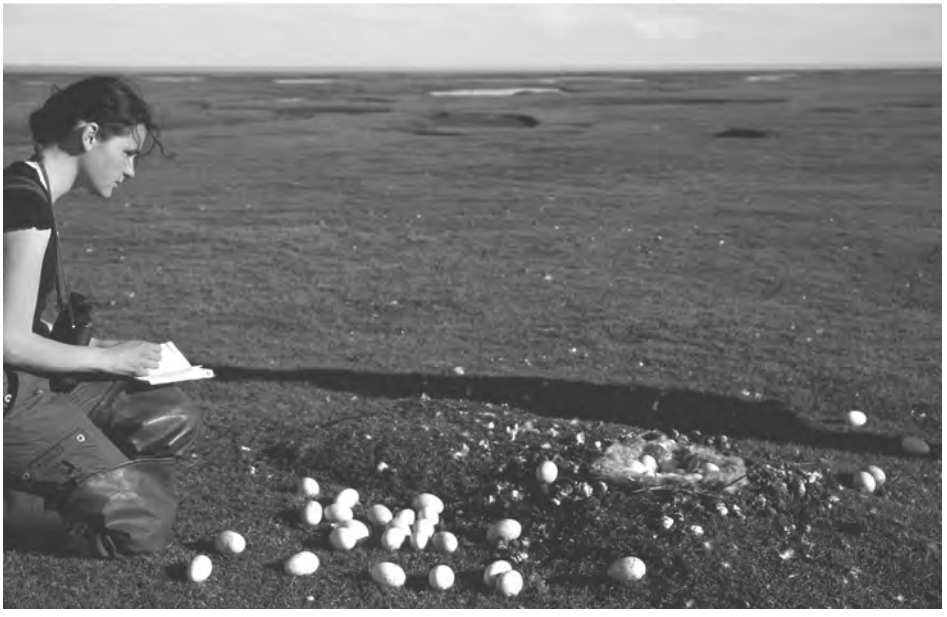


Figure Box B.1. Distribution of total fat extracted from dissected tissues or stores and the rest of the carcass. Columns represent 21 birds, sorted by their total fat mass relative to fresh body mass with values given below the columns. Tissues with similar and/or small fat contents were combined. Average fat contents and further measurements of individual tissues can be inferred from Table Box B.1.

leg muscles, heart and the 'rest' of the carcass containing the skeleton differed significantly between sexes (Table Box B.1). Fat was predominantly accumulated under the skin, in the abdominal cavity and as mesenterical fat attached to the intestine. Figure Box B.1 shows for each bird the relative contributions of fat extracted from various tissues, organ groups or stores to total body fat (birds are sorted along increasing total fat load). Skin fat, including subcutaneous fat, generally comprised the largest proportion of total body fat. Its relative contribution increased among the study birds until total fat loads of about 10% were reached. At that level skin fat represented 47% of all body fat and remained close to this value for increasingly fatter birds. It should be noted that part of the fat attributed here to pectoral and leg muscles belongs in fact to the subcutaneous fat layer which is attached to these muscle tissues and could not always be completely removed (especially from leg muscles) during dissection. A considerable amount of fat was not attached to distinctive dissectible organs or stores as specified here, but was distributed in the 'rest' of the carcass. Its relative contribution to total fat diminishes as fat depots under the skin and in the abdominal cavity build up. Like skin fat, the fraction of abdominal fat correlated positively with total fat loads (skin fat $r = 0.69$, $P < 0.01$; abdominal fat $r = 0.76$, $P < 0.001$). Relative contributions of fat from other tissues/tissue groups showed either no correlation (intestines; liver + kidneys + spleen) or decreased with increasing total lipid loads, as for heart + gizzard ($r = –0.49$, $P < 0.05$) and for flight + leg muscles ($r = –0.58$, $P < 0.01$).

The water content of the fat-free mass H_2O_{FFM} was approximately 75% in most tissues, except in skin and rest of the carcass containing the skeleton (Tabel Box

B.1). We have no explanation for the relative high water content in the H_2O_{FFM} of abdominal fat, however, also Pace and Rathbun (1945) noted a high value (82%) in adipose tissue. The relative low value for flight muscles compared to other muscle tissue reflects most likely the long exposure to evaporative loss during the time consuming removal of the skin. Comparative data are available from carcass analysis of Canada geese *Branta canadensis minima* measured at various stages (n = 8-9) throughout the annual cycle (Raveling 1979): average water content in H_2O_{FFM} of flight muscles was 73.2% (females), 73.6% (males) and in the liver 73.8% (females), 74.1% (males), resembling our values. Also fat content of these two tissues in Canada geese was very comparable to our data: 2.9% (females) and 2.6% (males) in flight muscle and 3.4% in liver (same for both sexes), when excluding the pre-laying period. Average liver fat contents were almost invariant during all other stages but peaked at 3-4 times higher values in both females and males during the pre-laying period (Raveling 1979).



Part

II

Travel to breed

Chapter

3

Spring stopover routines in Russian barnacle geese *Branta leucopsis* tracked by resightings and geolocation

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Ardea (2006) 94: 667-678

Abstract

By attaching 9-g loggers (recording dusk and dawn times to a memory chip) to the coded leg rings of barnacle geese *Branta leucopsis* caught in a breeding colony at Tobseda (68°35'N, 52°20'E) on the arctic coast of the Russian Federation in 2003 and by their recapture and retrieval in the 2004 season, we reconstructed the year-round movements of 19 females. We analysed spring migration movements of logged birds until they entered the zone of continuous daylight (c. 20 May), supplemented by ring reading in the colony. The technique also enabled description of incubation rhythm in these arctic breeders, allowing inferences about attempt and timing of breeding without the necessity of direct observation. Although the birds did not necessarily travel together, most travelled on 14–15 (9 individuals) and 17–18 May (10 birds) when favourable conditions for long-distance flights prevailed. The majority of birds remained in the Wadden Sea well into May, and only 6 staged more than a week anywhere in the Baltic (median staging period 4 days). The majority reached the White Sea by mid-May (latest 23 May) after which near-continuous light precluded further locations. Most tracked individuals spotted in the colony arrived during 6–11 June (mean 8), on average 4 days before first egg date. The median laying date for 17 'logger' birds (from direct observation or back-dating from start of incubation) was 13 June (range 5–19), the same as for the colony as a whole in 2004 (n = 385). We conclude that most Tobseda birds tend to overfly the Baltic, and eastern White Sea staging areas are used for on average three weeks before arrival at the breeding colony. Judging from the timing in 2004, rapid follicular development must commence at pre-colony staging sites, and from observations in 2002 we suspect these to be on the Kanin Peninsula 360 km W of the nesting area. The barnacle geese from the newly established Tobseda colony have apparently pioneered a modified spring migratory routine, possibly partly under the influence of their shorter travel distance. The extended stay in the Wadden Sea fits with the trends in May census data over the past 15 years and may indicate that spring feeding conditions are better than formerly, that the Baltic staging sites are filled to capacity, or some combination of these factors.

Introduction

Geese and swans have played a pivotal role in discussions of the constraints (nutrients, weather) acting on the timing of breeding. Arctic breeding species have attracted particular attention since the penalties of late hatching young were evocatively documented by Barry (1962). Apparently early laying is crucial, forcing females to lay eggs well before local forage plants start spring growth (Prop and de Vries 1993). Early breeding confers enhanced success and has been assumed to depend at least in part on the 'import' of body stores of fat and protein accumulated at more southerly staging sites or even in the wintering area (outlined by Newton 1977). Early evidence that 'body condition' at arrival was critical to nesting success was derived from carcass analysis of birds collected at various intervals through breeding (reviewed by Rohwer 1992) and more recently by following the fates of marked individuals whose nutritive status is revealed by observation of the API (Abdominal Profile Index). Madsen et al. (pers. comm.) show that Pink-footed Geese APIs at departure from northern Norway staging sites – the last major stopover before the flight to breeding areas on the Spitsbergen archipelago (Glahder et al. 2006) – predicts not only subsequent breeding success but also their prospects of individual survival through the summer and both migratory journeys (as deduced from resightings in the autumn). Analysis of stable isotope ratios in dietary foods and body organs or products of the birds enables us to trace the origin of the nutrients laid down in the eggs. Such new techniques help to discriminate between 'exogenous' (i.e. locally collected) and 'endogenous' (i.e. flown in by the parent birds) nutrients invested in reproduction and enable an assessment of the degree to which individuals adopt 'income' versus 'capital' breeding strategies (see Nager 2006).

In the light of this debate it is of considerable interest to obtain individual spring migratory schedules of females known to breed afterwards. Ideally, these timetables should be accompanied by information of foraging conditions (and accumulation of nutrients) at the various staging sites. As a first step along this road, we here present records on the spring migration of 19 female barnacle geese followed by a combination of position loggers and visual observations at the destination in the breeding colony. All but one laid eggs in the season of observation (2004), the remaining bird was inadvertedly shot upon arrival at the colony. Reconstruction of events elsewhere along the migratory route depends on observations both in the same and recent seasons. The focus upon one specific colony where all birds were originally marked (2003) was because this site is one of the relatively new nesting sites on the mainland coast of arctic Russia colonized in recent decades. We were interested in comparing the itinerary of individuals from this expanding population with the more traditional routines described from earlier reconstructions from ringing and observational data (Ganter et al. 1999).

Study sites and methods

Our study colony is situated on the Kolokolkova Bay salt marshes on the west coast of the Pechora Delta, adjoining the nearly abandoned village Tobseda (68°35'N, 52°18'E), on a peninsula bordered by the Barents Sea to the north and the Kambalnichya Pakha Gulf of the Kolokolkova Bay to the south. In the past decade barnacle geese *Branta leucopsis* have colonized the area (Syroechkovsky 1995; Van der Jeugd et al. 2003) where c. 1400 to 2100 breeding pairs have been counted over the last three years, including up to 1000 pairs on islands in the north of the bay 5 km off the coast. Numbers of moulting geese can exceed 10 000 adult birds (at least one year old) as the area also attracts non-breeders and failed breeders from elsewhere. Van der Graaf et al. (2004) describe the habitats and their use by geese (small numbers of White-fronted *Anser albifrons* and Bean *Anser fabalis* Geese also nest). Between 360–594 barnacle geese have been ringed annually since 2002, including 130–319 adult birds with colour rings. Geese were captured on the nest and by rounding up flightless birds during moult, marked with metal rings (Moscow) and a sample of birds also fitted with individually inscribed coloured leg rings (one on each leg) allowing identification at distances up to 250 meters. By the time of the analysis presented here (spring migration 2004), 558 adult birds had been colour-ringed in this population.

We used GLS (Global Location Sensing) technique based on logging diurnal changes in light levels (Wilson et al. 1992; Hill 1994) to track annual movements of female barnacle geese belonging to the Tobseda colony (another common term for this technique is "light-level geolocation" or just "geolocation"). Archival tags equipped with a 'clock memory chip' record light intensities to calculate the precise time of dusk and dawn to estimate geographical positions (two fixes daily); day (night) length determines the latitude and time of local midday (midnight) the longitude. GLS loggers were fitted on 54 female barnacle geese during breeding or moulting in 2003. Most (38) were caught on the nest, to ensure local breeders and enhance the chance of observing and re-capturing them in subsequent years. All of the additional 16 birds caught during moult had brood patch traces and 6 were known to have bred earlier in the same season. The 9 g logger (for details see Afanasyev 2004) was attached to one of the plastic rings around the legs (see Fig. 3.1). Total mass of logger and all rings was 21 g, corresponding to 1.5% of females' body mass at the end of incubation. Retrieval of the information necessitates recapture of birds, and the data presented here derive from 19 female 'logger birds' out of 24 recaptured in 2004 (1 shot, 16 caught on the nest, 7 caught during the moult); 5 loggers failed to download. After downloading loggers were replaced on the same birds or attached to new ones. In total 39 'logger birds' were spotted or caught in the wider study area in 2004, over the period from arrival of the first geese until mid of moult. For birds that were not seen breeding or caught during moult, it was often impossible to establish if they had bred and lost clutches or young or did not bred at all. It will be noted that a substantial part of breeding birds were located on islands (see above), and we visited these colonies only once during late incubation for most of the birds.

Figure 3.1. Female Barnacle Goose carrying a GLS logger attached to the left leg rings (photo H. van der Slot). The GLS unit weighs 9 g and its dimensions are 22x19x12 mm (further details in Afanasyev 2004).

The loggers measured light intensity every 1 min, but only recorded the maximum value of 10 successive readings (i.e. within each 10 min interval) together with the corresponding time at the *end* of that 10 min interval. This can lead to a potential mismatch of time and light value during the dusk period by up to 10 min, because then the maximum light value is more likely to be measured at the *begin* of a 10 min interval. The program used to process the light data (i.e. 'MultiTrace' by Jensen Software Systems) had been adjusted to account for that problem. 'MultiTrace' provides a full visual control throughout the analyses enabling the identification and improvement of obviously erroneous sections. Nevertheless, subsequent removal of spurious position estimates apparently associated with light level interference is usually necessary in geolocation (e.g. Phillips et al. 2004). This was almost unnecessary here, where the major objective was to reconstruct the timing of large scale movements between discrete known staging areas, rather than produce an accurate description of the precise migratory route. Geographical coordinates generated by MultiTrace were smoothed 4 times and imported into ArcView GIS 3.2 (ESRI) to map the routes shown in Fig. 3.2, although we used the unsmoothed coordinates, in particular the values for longitude, for the determination of dates of shifts between major staging areas. GLS loggers of the same type and manufacture were evaluated during a study on seabirds (Phillips et al. 2004); positions of free ranging albatrosses could be determined with a mean error ± SD of 186 ± 114 km.

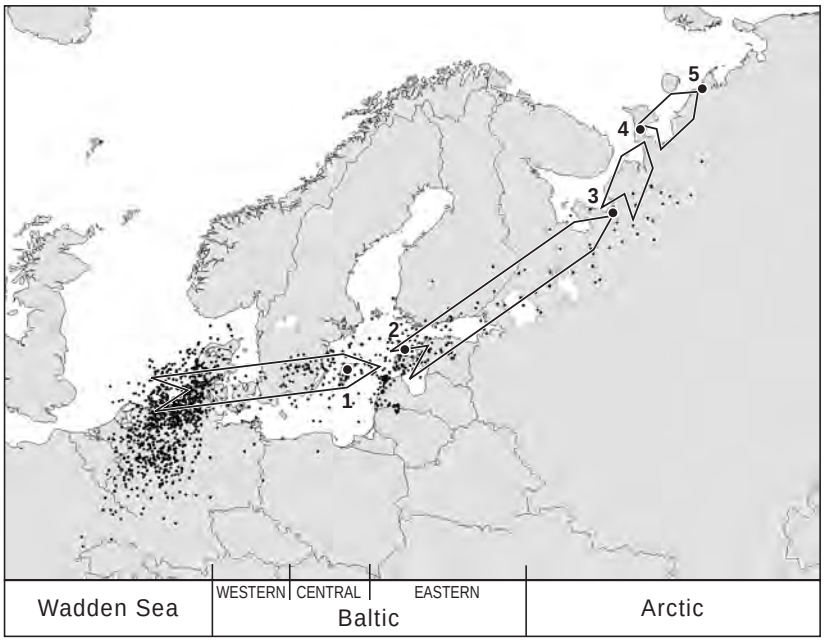

Figure 3.2. Position estimates derived from GLS loggers. Plotted are smoothed (4x) positions (two per 24 hrs) for 19 female Barnacle Geese from 15 April onwards until geese encountered light conditions precluding position determination by GLS (see text for details). Also shown are the defined geographical regions as applied in Fig. 3.3 and the text. Specific staging sites along the spring migratory route after geese left the Wadden Sea are denoted by 1 = Gotland; 2 = Estonia; 3 = mouth of the river Dvina; 4 = Kanin Peninsula. Number 5 marks the location of the breeding colony. The map is in a north pole Lambert azimuthal equal-area projection centred along the 30° E meridian.

One drawback inherent in the method is the increased latitudinal error close to the equinox, especially the winter side of the equinox (Hill 1994; Ekstrom 2004). We have therefore omitted readings around the vernal equinox (21 March), but fortunately most movements dealt with here stem from late April onwards. Moreover, the migratory journey is largely a west-east movement along coastal lines, so longitude estimates can reveal much about the major shifts. A second limitation is that the GLS system requires at least a few hours of darkness to enable geographical fixes, hence measurements ceased when birds crossed the Arctic Circle in late May. At the latitude of our study area (and of the nearest penultimate staging site on the Kanin Peninsula) nights are no longer 'dark' after 28 March (all-night astronomical twilight) and the sun remains continuously above the horizon from about 26 May to 18 July (Anonymous 1996).

Our party of 6 observers was in the field 24 May – 17 August 2003 and 28 May – 19 August 2004. Migration watches were kept daily until mid-June (7 hours contin-

uous observation, longer if heavy movements occurred) and ground counts in the colony area undertaken whenever weather allowed. Three observation towers were manned daily to watch for ringed birds in the colony area (using 20–60x telescopes), which is less than 500 meters wide. Nest searches were conducted periodically by 3–5 observers walking abreast to minimise disturbance, and nests marked with tagged bamboo sticks to ease observation from the towers. Laying date was recorded from direct observations during the laying period or backdated from hatch. For females carrying data loggers, it can also be backdated from the start of incubation, which often coincided with laying of the third egg (own observations), and the incubation rhythm detected in the light-level data. Differences in estimating the laying date following this method compared to direct observations were in the range of 0–2 days.

In 2002, we camped at the Shoina salt marsh (67°53'N, 44°08'E) on the Kanin Peninsula 360 km west of the Tobseda site from 20 May to 15 June, where we discovered that this recently colonized marsh (Filchagov and Leonovich 1992) is also an important spring staging site for more than 25 000 barnacle geese. These observations give insight into the conditions our logger birds might have encountered before arrival in the colony.

Results

Birds fitted with GLS loggers followed the general spring migration route as described for the Russian Barnacle Goose population (Fig. 3.2, Ganter et al. 1999). The species is found in coastal areas all year round, and primarily follows coastlines during its migrations. Points mapped here at any great distance from the coast reflect the limited accuracy of the tracking system (see methods) but reliably reveal major displacements. The tagged geese showed distinct shifts between major staging areas, here defined as (1) the Wadden Sea which largely overlaps with the wintering area, (2) Baltic Sea, subdivided into West (Sweden and Denmark W of Öland), Central (Öland, Kalmar Sund and Gotland and East (Estonia and S Finland) and (3) Arctic (White Sea and east of it). Only the SW portion of the White Sea fell within the discriminatory function of our logger system. Our observations (Fig. 3.2) suggest that this zone was hardly used as a stopover site by barnacle geese, which apparently headed for staging sites further northeast after leaving the Baltic. We have therefore distinguished Wadden Sea, Baltic and Arctic as the major stopover areas and have assembled the information for the 19 logger females diagrammatically in Fig. 3.3. All but one bird (no. 1), which had already departed from the wintering grounds on 23 March, left the Wadden Sea in May. Median departure date for all 19 females was 14 May, and median stopover duration in the Baltic area was 4 days. The 180 ‘goose days’ spent by these 19 birds in the Baltic were divided between the Western 13 (6.9%), the Central 54 (30%) and the Eastern Baltic 114 days (63%), showing the preference for Estonian staging sites. After a mass departure on 17 May (involving 9 of the 13 birds then in Estonia) 60% of the logger birds

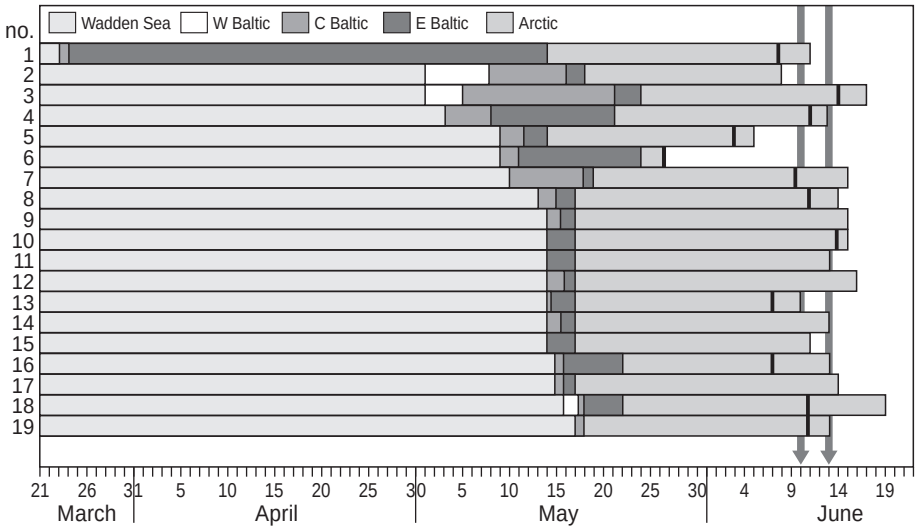

Figure 3.3. Spatiotemporal pattern of 19 females in the period March to June 2004. Patterns represent staging areas in the Wadden Sea, the Baltic Sea (separately for West: W of Öland; Central: Öland, Gotland and adjacent mainland; East: Estonia, Finland) and the Arctic until start of laying (except for no. 6, which was shot upon arrival at the breeding ground). Black bars within the Arctic period denote arrival time at the breeding site, known for 12 birds from direct observations. The left arrow marks the mean date of first observation at the breeding site of 80 individually ringed adult geese (excluding the loggers), and the right arrow marks the mean laying date for 385 nests monitored in 2004 (see text for details). The individual cases are sorted by departure time from the Wadden Sea.

had left the Baltic and were on their way to Arctic Russia. On this same date the last straggler from the Wadden Sea reached the central Baltic (no. 19) and bird no. Eighteen moved from the western Baltic to the central Baltic, so in all at least 11 of our birds engaged in major movements on that date (and two more undertook major displacements on 18 May). The majority of our tracked birds reached the White Sea by 18 May (after adding 1 day of flight from the Baltic) with the latest on 25 May. The last mass departure of barnacle geese from the Dollard area on the German-Dutch border (where many Tobseda geese have been identified) occurred on 13–15 May, when major departures also occurred from Schleswig- Holstein near the northern extreme of the Wadden Sea (K. Koffijberg and K. Günther, pers. comm.). A massive passage along the Gulf of Finland was observed during for 17–19 May (P. Tolvanen, pers. comm.) coinciding with those of our sample.

At the Tobseda breeding colony the main arrivals of barnacle geese took place on 4, 6 and 10 June, with a late influx on 15 June. The mean date of first observation of individually ringed adult geese (excluding the loggers) identified until 16 June, when 97% of all nesting birds initiated their clutch, was 10.0 June (SD 4.7, n = 80). The mean first observation (presumed arrival date) for 12 geese fitted with GLS

loggers was 8 June, and most arrived between 6 and 11 June. Of the 19 females, one was shot by local hunters the day of arrival (26/27 May, the earliest in our sample, having left the Baltic 1800 km distant as late as 24 May) when only a few tens of barnacle geese were present. Of the remaining 18, 17 actually bred, and one probably attempted to do so but lost its clutch early on (as inferred from the logger trace). After arrival, on average 4 days elapsed before the first egg was laid. The peak date for first eggs (clutch initiation) was 12.8 June for the sample of logger birds (SD 3.3, n = 17) and was 12.4 June (SD 2.7, n = 385) for all Barnacle Goose nests monitored in 2004.

Comparing these data from the colony with the departure dates from the Baltic it can be concluded that on average 25.8 days (SD 2.6, n = 17) were spent somewhere in the Arctic prior to laying (22 days in the Arctic before arrival at the colony). The logger birds closely match the time pattern of spring migration of their conspecifics at the colony and it is noteworthy that virtually all laid eggs in 2004. The late departure from the Wadden Sea is also born out by visual observations on other ringed birds from the colony. For example, 12 adult individuals (excluding 'logger birds' reported here) were identified as late as on 11 and 13 May in the Dollard area on the Dutch-German border among thousands of barnacle geese. The rather short stay in the Baltic and the preference for the eastern Baltic coast is mirrored in only one observation of a ringed Tobseda family on the island of Gotland on 22 April despite thorough searching during April and May. The nesting success of 18 'logger females' (shot bird excluded) in 2004 was recorded as follows: 5 nests hatched; 3 survived at least until trapping, but were not further observed; 4 failed breeding at a late stage due to catching (nest predation or desertion); 6 failed at some stage during incubation for unknown reasons. The last group, which apparently failed for other reasons than human interference, presents 33%, and this is not far from the 25% failure rate of all monitored nests (n = 735).

Fig. 3.4 shows the relationship between departure date from the Baltic and the laying date at the Tobseda colony, and demonstrates that late departure is reflected in later laying. Although there seems to be a slight 'speeding up' effect (the slope is less than one day per day delay in Baltic departure) the general finding is that the interval between these events is almost always close to 25 days, equivalent to the pre-nesting staging time in the Arctic (the range was 21–30 days). Another way of displaying these data is to plot events in relation to the date of departure from the Wadden Sea (Fig. 3.5). We now see that birds departing late from the Wadden Sea shortened their staging time in the Baltic (bird no. 1 departing from the Wadden Sea already in March spending 52 days in the Baltic, and the latest departing bird, no. 19, leaving the Wadden Sea on 17 May and reducing its stay in the Baltic to a single day). Baltic staging (range 1–52 days) is thus highly variable and clearly date-dependent. The time spent in the Arctic before egg-laying, on the contrary, was independent of departure date from the Wadden Sea and averaged 26 days. It will be noted that, excluding the extremely early arrival, our logger birds generally spent not more than three weeks in the Baltic (more than half spent less than one week), i.e. less than the final staging period in the Arctic.

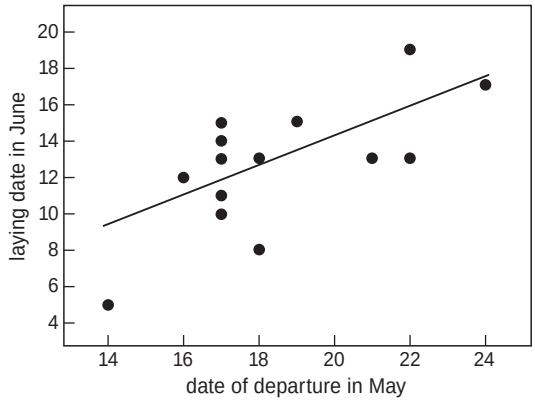

Figure 3.4. Relationship between laying date (first egg) and date of departure from the Baltic (rate of delay 0.75day day^{-1}, $F_{1,15}$ = 9.93, P = 0.007).

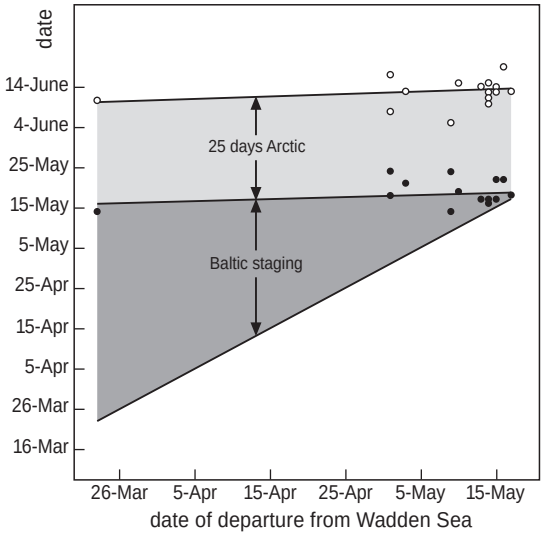

Figure 3.5. Stopover duration in the Baltic (dark grey coloured area) and in the Arctic prior to laying (light grey area) in relation to departure from the Wadden Sea. Black dots represent individual departure dates from the Baltic; open circles mark individual laying dates. Birds shortened their stopover time in the Baltic in relation to departure time from the Wadden Sea ($F_{1,17}$ = 283.13, P < 0.001), whereas neither pre-nesting time in the Arctic nor laying date was related to different departure dates from the Wadden Sea ($F_{1,15}$ = 0.01, P = 0.921 and $F_{1,15}$ =0.70, P = 0.416, respectively).

Discussion

The light-weight GLS loggers applied together with leg rings to female barnacle geese (c. 1% of body mass) do not appear to have inconvenienced the birds in any way. Resighting probabilities of the 38 'logger birds' that were caught on the nest in 2003 and 41 female birds that where wearing similarly coloured rings but no loggers and were seen nesting in 2003 were comparable both in the wintering area (2003/2004, $\chi^2_1 = 0.0486$, $P = 0.83$, and in the breeding colony during the subsequent summer (summer 2004, $\chi^2_1 = 0.6318$, $P = 0.43$). The timetable of the tagged and recaptured birds conformed to that of the other geese in the colony and the 18 survivors all also laid eggs within the normal time window (it will be recalled that one was inadvertedly shot upon arrival). We will therefore assume that the data obtained are representative for breeding birds of our study colony. However, we refrained from analyses including breeding success, because this was too much affected by human interference (e.g. nest catches).

The Russian-Baltic Barnacle Goose population, of which Russian Arctic breeders comprise more than 90%, has shown a steady increase of about 7% annually since 1960 (Ganter et al. 1999). Improved protection measures throughout its range and favourable changes in agricultural practice have been considered responsible for this development (Ebbinge 1991; Van Eerden et al. 1996; Van Eerden et al. 2005). Islands in the Baltic have been a traditional spring staging area for the species, documented by registrations in western Estonia going back at least to the beginning of the 20th century (Loudon and Buturlin 1908; Kumari 1971). On the Estonian islands and adjacent mainland barnacle geese are present in considerable numbers from early April until 25 May (Leito et al. 1991). Until the early 1990s, the increase in numbers of spring staging barnacle geese in Estonia paralleled the increase of the total population, and on average close to 50% of the individually marked birds from the Wadden Sea had been observed in spring in Estonia (Leito et al. 1991). After a dynamic phase of expansion of the Barnacle Goose into new staging sites Leito (1996) concludes that all potential sites in Estonia have been occupied by the mid 1990s, and the continued increase in goose numbers resulted in higher feeding pressure. In response, the growth of the Estonian spring population of the Barnacle Goose levelled off, with numbers fluctuating around 120 000 since the mid 1990s (Leito and Truu 2004). Compared to total flyway numbers, which totalled 360 000 barnacle geese in 2000 (Delany and Scott 2002) Estonia is apparently being used by at most about one-third of the population during spring at present. Alternatively, the staging time in Estonia might have become curtailed, leading to a higher turnover rate not evident from the total present at any one census. In the years 1983–1991 Leito (1996) collated the sightings on individually ringed barnacle geese and showed that the stopover time was only 4 days (SD 1.3, n = 65, range 1–21), although the actual staging period probably lasted longer. Eighteen of our 19 logger birds visited Estonia in May 2004 for a median stopover duration of 3 days and only three stayed longer than one week (13, 13 and 51 days). For most of our geese the Estonian stopover in 2004 could make only a small contribution towards migratory costs.

The modest use made by our tagged birds of western and central Baltic sites came as a surprise. Although 16 of our 19 geese stopped off on Öland or Gotland, the median stopover duration was again only 3 days (three birds staying longer than one week: 8, 8 and 16 days) and only three birds made stopovers in the western Baltic (2, 4 and 7 days). Although there are no total count data available for Gotland, a major staging site in the central Baltic, local farmers have not noticed any increases over the past decade. That Gotland is already being used to capacity can also be concluded from studies on the spring feeding ecology of barnacle geese during staging in 2003 and 2004 (Van der Graaf et al. 2006b). The grazing pressure reported was more than twice the value at a comparable staging site in the Dutch Wadden Sea, and at Gotland goose grazing right from the onset of spring growth prevented a substantial accumulation of fresh biomass over the entire stopover period.

Systematic total censuses have revealed that an increasing proportion of the flyway population has remained in the Wadden Sea during May in the 1990s (see Fig. 3.6). If we accept that one-third of the flyway population of 360 000 was still in the Wadden Sea in May 2000, this would equate to 120 000 birds, leaving approximately 240 000 barnacle geese elsewhere (judging from our tagged birds virtually all of these in the Baltic). According to Fig. 6, before 1993 the entire flyway population had already moved to the Baltic in May, close to 200 000 at that time (Ganter et al. 1999). We conclude that since the mid 1990s the Baltic spring staging sites have absorbed only a part of the population increase and may well be reaching capacity.

That only 2 of our tagged birds stayed longer than three weeks in the Baltic, compared to 13 (68%) that stayed not longer than a week, with over half (11 birds) staying behind in the Wadden Sea until 14 May, fits the trend for the flyway population as a whole. Evidence that prolonged spring staging in the Wadden Sea had already set in during the late 1980s has been presented by Stock and Hofeditz (2002) on the basis of departure dates from the Hamburger Hallig on the west coast of Schleswig-Holstein (northern Wadden Sea). Koffijberg and Günther (2005) updated this information and showed that the Barnacle Goose has delayed its departure by more than six weeks over the past 15 years (Fig. 3.7). This regular progression is evident throughout the period of observation, and our tagged birds reflect the overall pattern. Individuals were much more restricted in their decision when to take off for the Arctic compared to the temperate staging area (Fig. 3.3 and 3.5), and this climatic restriction seems also responsible for the low annual variability in the timing of spring migration at the Gulf of Finland, the 'exit' out of the Baltic (Fig. 3.7). Some variation, however, exists, and at least a tendency ($F_{1,13} = 3.7$, $P = 0.08$) towards earlier departure from the Baltic over the past 14 years can be noticed, which is likely to be driven by a climatic change towards an advanced onset of spring.

Geese that left the Baltic later started clutches later (Fig. 3.4), so despite the adjustment of stopover duration according to departure time from the Wadden Sea apparent in Fig. 3.5, they did not compensate for a delayed Baltic departure by reducing pre-nesting staging time in the Arctic. This underlines the importance of

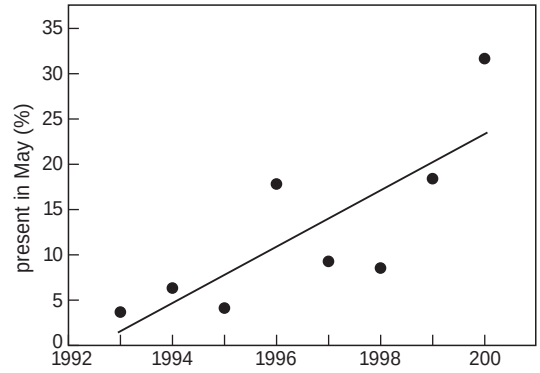

Figure 3.6. Numbers of Barnacle Geese present in the international Wadden Sea in May, expressed as percentage of the Russian-Baltic flyway population (r = 0.8, P = 0.019, redrawn after Koffijberg and Günther, 2005).

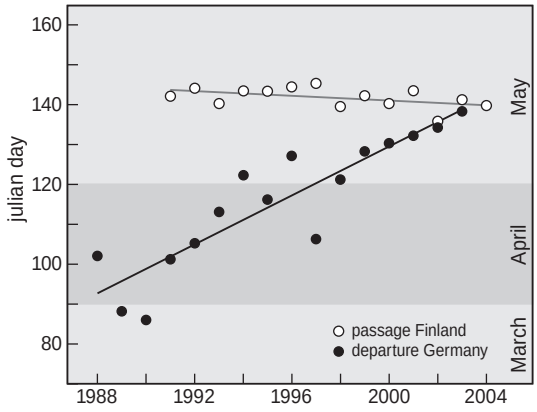

Figure 3.7. Date of mass departure of Barnacle Geese at the Hamburger Hallig, Schleswig-Holstein, Germany, in the years 1988–2003 (rate of increase 3.04 day year^{-1}, $F_{1,14}$ = 57.2, P < 0.001, redrawn after Koffijberg and Günther, 2005) and median date of mass passage at the Gulf of Finland ($F_{1,13}$ = 3.7, P = 0.08, data obtained from the Kymenlaakso Birding Society (1990–2004), annual reports published in Lintukymi and from P. Tolvanen (for spring 2004, pers. comm.).

arctic pre-nesting staging sites, where the geese can accumulate body stores at a high rate. barnacle geese were able to reach fat deposition rates of c. 30 g day^{-1} at spring staging sites on the Kanin Peninsula in 2002 (Eichhorn et al. unpubl.), where we suspect rapid follicular development commences, 360 km from nesting area.

The increase of the Russian Barnacle population coincided with a pronounced westward expansion of its breeding distribution (Ganter et al. 1999), thereby shortening the migration route by up to 700 km (e.g. for birds breeding on Kanin

Peninsula compared to Vaigach or Novaya Zemlya). Reductions in migratory costs may have facilitated a new migratory strategy while reducing the importance of an intermediate staging in the Baltic. The Tobseda birds studied here belong indeed to a new breeding site colonised in the early 1990s (Syroechkovsky 1995), 300–400 km southwest of the traditional breeding area.

Accepting that the Baltic sites are now filled to capacity, the trend to use other areas would be explained by changing travel traditions. Geese experiencing a migration pattern that does not result in successful breeding in one spring would likely change their patterns of site use the following year such as documented for the Pink-footed Goose by Madsen (2001). There remains the intriguing possibility that spring feeding opportunities in the Wadden Sea have improved over past decades. Aside from climatic amelioration the extended grazing of the geese themselves may prolong the profitable phase of the vegetation in the Wadden Sea in spring as concluded for the Brent Goose by Bos et al. (2004) and for the Barnacle Goose by Van der Graaf et al. (2002). Perhaps these two processes have together enhanced the prospects of prolonged Wadden Sea staging. It would be of great interest to ascertain the spring staging pattern of barnacle geese from the long-established traditional colonies on Vaigach or Novaya Zemlya that possibly still follow the 'Baltic routine'. Observations on barnacle geese of the Svalbard population on staging islets in northern Norway have confirmed feeding territoriality and the dominance of long-term site visitors (Prop 2004) and this would argue for 'grazing rights' of the original population. For species like geese where migration routes are transmitted culturally by the family there is ample scope for flexibility (Sutherland 1998). Assembling more such case histories of individual barnacle geese is bound to be rewarding.

Acknowledgements

We thank all fieldworkers, and Konstantin Litvin in particular, for their assistance in the field. We are grateful to Julia Stahl and Mennobart van Eerden for their various help in the organization and support of the Russian Arctic expeditions. Petteri Tolvanen helped to retrieve data on goose passage over Finland from reports of the Kymenlaakso Birding Society. Jeroen Creuwels and Rory Wilson stimulated the work with GLS loggers, and Jochim Lage gave helpful advice during the process of light-level data analysis. Financial support was provided by the Dutch Institute for Inland Water Management and Waste Water Treatment RIZA, the Schure-Beijerink-Popping Fonds and the University of Groningen. The European Science Foundation (BIRD programme) awarded travel grants to GE and HvdJ. GE was supported by scholarships from the 'Marianne und Dr. Fritz Walter-Fischer Stiftung', Germany, and the 'Ubbo Emmius Programme' at the University of Groningen.

Chapter

4

Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese

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Submitted

Abstract

Since the early 1990s an increasing proportion of barnacle geese, *Branta leucopsis*, bound for breeding sites in the Russian Arctic delay their departure from the wintering quarters in the Wadden Sea by four weeks. These late-migrating geese skip spring stopover sites in the Baltic traditionally used by the entire population. Individual geese tracked by satellite or light-level geolocators during spring migration 2004 and 2005 predominantly followed the new strategy, but a minority still maintained the traditional pattern. Between years six individuals were consistent in their migration strategy but one switched between strategies. Despite a spread of more than 50 days in departure date from the Wadden Sea both early and late departing females laid their eggs within the nine day time-window conferring breeding success. The spread of these new migration routines coincided with a strong increase of overall numbers and the exploitation of new spring staging resources in the Wadden Sea. Counts from Estonia demonstrate that numbers have levelled off recently at the Baltic staging sites, suggesting that the capacity of these staging sites in spring has been reached. Although onset of spring affects migratory timing in barnacle geese, it cannot explain the observed delay in departure from the wintering grounds. We hypothesise that the new migratory strategy has evolved in response to increased competition for food at spring staging sites in the Baltic. According to an analytical model of optimal migration, the geese should skip the Baltic whenever the energy deposition rate falls below 88% of the Wadden Sea value.

Introduction

Small avian herbivores such as geese select forage plants of high quality (in terms of protein content and digestibility) and it has been proposed that they time their spring migration to their arctic breeding grounds to match the spring flush of plant growth as it sprouts along their route (Drent et al. 1978; Van der Graaf et al. 2006b). Due to their direct dependence on plant forage, herbivores can be expected to show early and strong responses to climate change, which will alter feeding conditions at staging sites. The rate of nutrient acquisition and consequently body condition is known to influence migratory decisions (Weber et al. 1998; Drent et al. 2003; Prop et al. 2003). Both the timing of migration and body condition at arrival in the breeding grounds are crucial determinants of reproductive prospects (Kokko 1999; Bêty et al. 2003). Moreover, body condition as early as in the premigratory stage, when still on the temperate wintering grounds, can be decisive for success in the arctic breeding grounds (Ebbinge and Spaans 1995), indicating limited possibilities to compensate for deficiencies later on. Arctic breeding geese have to deposit resources in excess of what is needed to cover the flight costs. Strong seasonality of the arctic environment leaves only a narrow time window for successful reproduction. The growth period of the offspring needs to be tightly matched with local peaks of food resources (Lepage et al. 1998; Black et al. 2007). During egg-laying and early incubation local food resources are still scarce. Furthermore, incubation tasks minimize foraging opportunities for the female (Afton and Paulus 1992; Bowler 2005) as daily nest attentiveness is usually above 90%. Therefore, arctic geese arrive at the breeding grounds with a substantial surplus of endogenous nutrient reserves. They are doomed to fly in 'capital' gathered at spring staging sites (Drent et al. 2007).

Such a strategy does not minimise the energetic costs of migration, as flight costs increase inevitably with body mass (Pennycuick 1975). Energy-minimising migrants should travel with minimal loads between subsequent fuelling site (Alerstam and Lindström 1990). However, when time to gain adequate breeding condition is included in the time minimisation argument, overloading is in accord with time selected-migration. Birds may start breeding earlier through overloading at the last staging site as long as the increased costs on flight economy are more than counterbalanced by a higher rate of nutrient deposition at this staging site compared to the breeding site (Gudmundsson et al. 1991; Alerstam 2006b). The same condition applies to a time minimising migrant when by-passing a potential staging site further upstream along the migratory route should be favourable, i.e. deposition rates at succeeding stopovers must fall below those at the departure site.

We here examine a thirty-year data set on migration of the barnacle goose along the Baltic route and compare these with population counts. By means of data on individual geese (tracked in two seasons) we are also able to test if individuals show flexibility of migratory strategies. Additionally, individual travel schedules were combined with observations of the same birds in the breeding colony allowing us to evaluate possible fitness consequences of migratory strategies. The monitoring of

the progress of avian long-distance migration, at individual level and its linkage to events in the breeding phase has so far only rarely been achieved (Madsen 2001; Bêty et al. 2003; Alerstam 2006a; Drent et al. 2007). Thus the main objectives of this paper are to: 1) describe the timing of spring migration of barnacle geese over the past decades in perspective of a growing total flyway population as well as differences in the onset of spring, 2) evaluate under which conditions bypassing of the Baltic may become beneficial in the light of optimal migration theory, 3) present individual spring itineraries and their variation between years, and finally 4) examine if the dichotomy of alternative individual spring migration strategies incurs differences in the timing of breeding.

Methods

Study population and study sites

Barnacle geese wintering along the North Sea coast in Germany and The Netherlands belong to a population breeding on the arctic coast of European Russia and two temperate breeding populations in the Baltic and The Netherlands (Ganter et al. 1999). Although the Baltic and Dutch populations have been growing rapidly since their establishment in 1971 and 1981, respectively (Larsson et al. 1988; Meininger and Van Swelm 1994) now together numbering 46 000 individuals, the Russian arctic breeding population is by far the most numerous, currently representing 90% of the common wintering population of more than 500 000 birds (Black et al. 2007). The geese feed predominantly on grasses, sedges and herbs utilising coastal salt marshes and, in temperate regions, adjacent agricultural pastures. On their migration to the breeding sites in the Russian Arctic barnacle geese make use of a number of major staging sites. The North Sea coast from the Netherlands to southern Denmark serves as an important pre-migratory fattening area. Many geese wintering in the western Wadden Sea move short distances to accumulate more body reserves in the north-eastern Wadden Sea prior to their take off to more distant sites in the Baltic, most notably in western Estonia and on the Swedish island of Gotland (Ebbinge et al. 1991; Leito et al. 1991). The longest leap to be made is between the Baltic and pre-breeding sites on the White Sea coast, crossing unsuitable habitat of boreal forests.

Traditional breeding areas of this population were restricted mainly to the islands of Novaya Zemlya and Vaygach in the eastern Barents Sea. Through expansion back down the flyway, since the 1980s breeding occurs now down to the eastern White Sea coast, 650 km westwards (Ganter et al. 1999). Figure 4.1 shows areas of wintering, staging and breeding and our study sites along the migratory route. Individual migratory itineraries and data on breeding biology were obtained from birds nesting in a colony near the abandoned village Tobseda (68°35'N, 52°18'E) situated on the Kolokolkova Bay salt marshes on the west coast of the Pechora Delta (for details about this breeding and moulting site see Van der Jeugd et al. 2003).

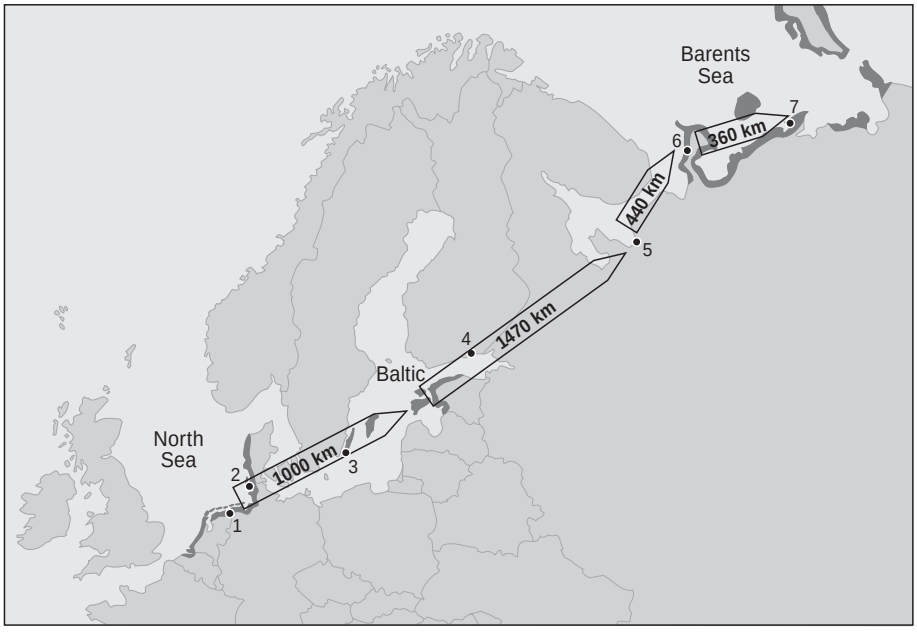

Figure 4.1. Map showing spring migratory route of Russian breeding barnacle geese with distances between staging sites and observation points: 1-Dollard estuary; 2-Wadden Sea; 3-Ottenby; 4-Finland; 5-Dvina delta; 6-Kanin Peninsula; 7-goose breeding colony at Tobseda. Dark grey shaded areas indicate wintering/staging grounds in the Wadden Sea and Baltic, and breeding grounds in the Russian Arctic.

Count and climate data

Estimates of the total flyway population were based on winter counts in the Wadden Sea from Ganter et al. (1999) and updated by SOVON, Dutch Centre for Field Ornithology. Spring staging birds in Estonia were counted by ground surveys in 1964, 1968, 1970 and from 1974 onwards by aerial surveys (in 16 years during 1974 – 2005; see Fig. 4.2). Censuses were conducted in the period 5–15 May using a constant census area and routine (since 1974) over the years and covered more than 90% of all sites known to regularly support 100 or more geese (Leito 1996). Data on timing of spring mass migration were gathered from three sites along the flyway. 1) Wadden Sea coast: Departure dates from the north-eastern Wadden Sea in Schleswig-Holstein, Germany (ca. 54°36'N, 8°52'E), when > 75% of the peak staging population had left the site were obtained from Stock & Hofeditz (2002) for 1988-1997 and updated with dates of mass departure from the same area for 1998-2003 (Koffijberg and Günther 2005) and 2005-2006 (Koffijberg pers. comm.). 2) Arrival in the Baltic area: Birds passing by the Ottenby bird observatory (56°12'N, 16°24'E) located at the southern tip of the Swedish island Öland were counted yearly in the period April–May. Data for the years 1970-2004 were extracted from

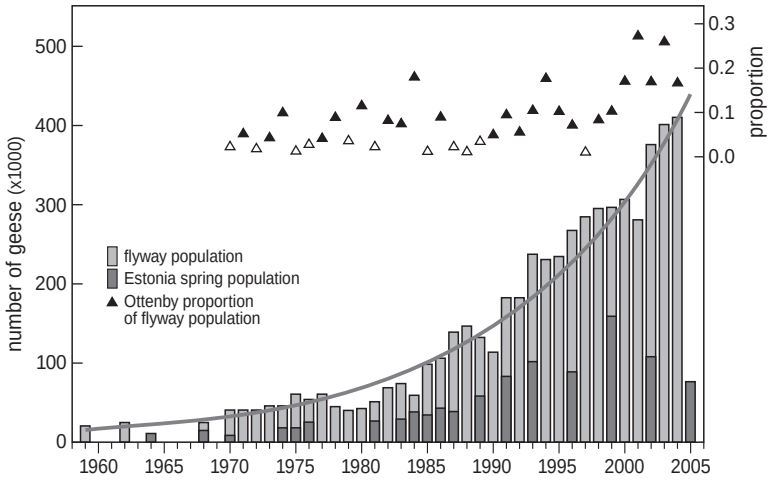

Figure 4.2. Size of flyway population and numbers of spring staging barnacle geese in Estonia depicted by columns scaled to the left axis. The equation fitted to the flyway population data (grey solid line) is $y = 13844e^{0.074x}$, $r^2 = 0.95$, corresponding to a yearly growth-rate of 7.7%. Triangles show the proportion of the total flyway population enumerated on spring passage at Ottenby with values given on the right axis. Open triangles mark years when less than 5% of the flyway population was counted at this observation point.

the observatory diaries. Ottenby is situated on a main migratory corridor for Barnacle as well as Brent geese *Branta b. bernicla* travelling from the Wadden Sea to Baltic staging sites (Green 1998). To assure a consistent representiveness we discarded years when < 5% of the flyway population was counted at Ottenby (Fig. 4.2). Information was updated from online reports of the Swedish Ornithological Society for barnacle geese passing through the southern province of Skania (http://www.artportalen.se/birds/default.asp) for 2005-2006. The day when ≥ 50% of the season's total passed through Ottenby and Skania, respectively, was taken as estimate for the arrival date in the Baltic. 3) Departure from the Baltic: Mass departure from the Baltic was estimated as median date from days with peak migration over the Gulf of Finland (at Kotka) as reported by the Kymenlaakso Birding Society in their annual reports (Lintukymi) for the years 1989–2004, and updated for 2005-2006 by Tolvanen (pers. comm.). We refrained from using census data recorded at Eemshaven, in the Netherlands, because these likely include substantial short-distance movements within the Wadden Sea.

Daily mean temperatures measured at Baltic and North Sea goose staging sites were gathered from the European Climate Assessment and Dataset (Klein Tank et al. 2002) for the period 1970-2006 for Vilsandi (58°23'N, 21°49'E) in western Estonia for all years but 1991, covered by data from Gotska Sandon (58°24'N, 19°12'E) and for Leeuwarden in The Netherlands covering 1970-1971. H. Vugts (pers. comm., Free University of Amsterdam) provided data for the Dutch island

Schiermonnikoog (53°30'N, 6°10'E) for 1972-2006. From the temperature data sets we calculated 'growing degree days' (GDD) by summing daily temperatures above a threshold value of 0°C over the period from 1 January until 12 April, the 'traditional' date of median arrival in the Baltic. GDD calculated with this threshold value is a good predictor for the onset of vegetation growth in temperate and cool biomes (Botta et al. 2000).

Observations on individual birds

We employed satellite tracking and Global Location System (GLS) data loggers (also called light-level geolocators) to track movements of individual barnacle geese breeding in our Russian arctic study site. We found no indication of impaired behaviour and/or condition in birds carrying tracking devices (for details see Eichhorn 2005; Eichhorn et al. 2006). Accuracy in the timing of movements is within a range of one day. We collated individual departures from the wintering grounds together with known laying dates for 21 birds in 2004 (all tracked by GLS) and nine birds in 2005 (one tracked by PTT, eight by GLS). For seven individuals spring migratory schedules could be recorded during both years.

Laying date (1st egg) was recorded from direct observations during the laying period or backdated from hatch. For females carrying data loggers, laying date could also be backdated from the start of incubation, which often coincided with laying of the third egg (own obs.), and the incubation rhythm detected in the light-level data. Data loggers were retrieved from captures during incubation and during moult. Median laying date for all monitored nests in the colony was 13 June in 2004 (n = 385) and 6 June in 2005 (n = 413). These dates were related to individual laying dates to calculate relative laying dates.

Results

Documenting the emergence of a new migratory behaviour

The barnacle goose population wintering in the international Wadden Sea has grown exponentially since a low in the early 1950s (Ganter et al. 1999), increasing at an annual rate of 7.7%, corresponding to a doubling time of 9.4 years (Fig. 4.2). Numbers of spring staging barnacle geese in Estonia followed the increase of the flyway population until the mid 1990s but then levelled off and are now decreasing.

Figure 4.3 shows long-term data of the timing of barnacle goose mass movements to and from the Baltic. Observations on departures in the wintering/pre-migratory area and on passage over southern Sweden correlate well ($r = 0.90$, $P < 0.001$, n = 15) and both illustrate a distinctive delay of departure from the wintering grounds, starting around the mid 1990s and stabilising during recent years. In contrast, mass migration along the Finnish coast, the "exit" of the Baltic, shows a remarkably stable timing over the past 18 years (21 May ± 3 days, mean ± SD), indicating that the interval between mass departure from the Wadden Sea and peak passage past Finland has decreased dramatically.

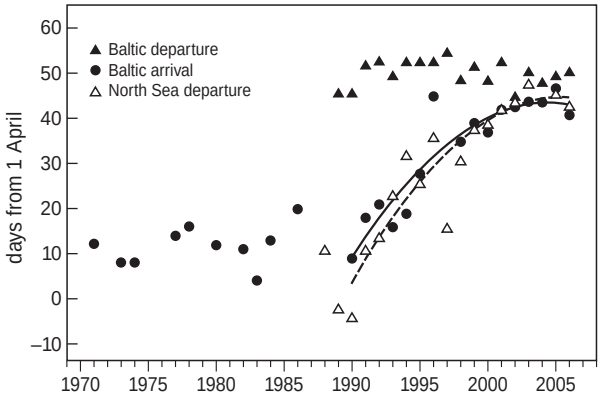

Figure 4.3. Passage dates along the migratory pathway: at the Finnish Gulf 1989-2006, over southern Sweden 1971-2006 and mass departures from the German North Sea coast 1988-2006. Curves fitted for the period 1990–2006 (with years renumbered to 1=1990 till 17=2006) refer to North Sea departure, broken line ($y = -0.175x^2 + 5.729x - 2.051$, $F_{2,13} = 33.16$, $r^2 = 0.84$, $P < 0.0001$) and Baltic arrival, solid line ($y = -0.162x^2 + 5.033x - 4.819$, $F_{2,13} = 42.44$, $r^2 = 0.87$, $P < 0.0001$); the quadratic term significantly improved the fit in both models.

Figure 4.4 presents a break-down of the Ottenby data illustrating the change of the seasonal dynamics of migration into the Baltic. During the earliest periods (1971-1984) more than half of the total number of birds passed Ottenby before 12 April. Delayed mass migrations became obvious from the second half of the 1990s onwards and resulted in an expansion of the migratory window. Beside the traditional mass movements in mid April, an increasing number of birds delayed their departure well into May. Since 2000 'April migrants' contribute only 20% of the numbers passing Ottenby during April-May, with the majority of the total flyway population leaving the Wadden Sea in the first half of May (peak close to mid May), four weeks later compared to before 1990.

Individual migratory schedules

To interpret the patterns illustrated so far, it is essential to investigate individual choices in the migratory schedule and their consequences. This is especially revealing for birds breeding in the same colony which share exogenous parameters like migratory distance, feeding conditions in the breeding grounds and optimal time of egg-laying. Employing both GLS and satellite telemetry, individual female barnacle geese tracked during spring migration of 2004 (n = 23) and 2005 (n = 12) confirm the two migratory strategies existing side by side (Fig. 4.5). Median number of days staging in the Baltic was four and three in 2004 and 2005, respectively. Departure from the Baltic (influx into the White Sea) of the tracked birds took place 14–27 May (median 17.5) in 2004 and 18-20 May (median 19.5) in 2005,

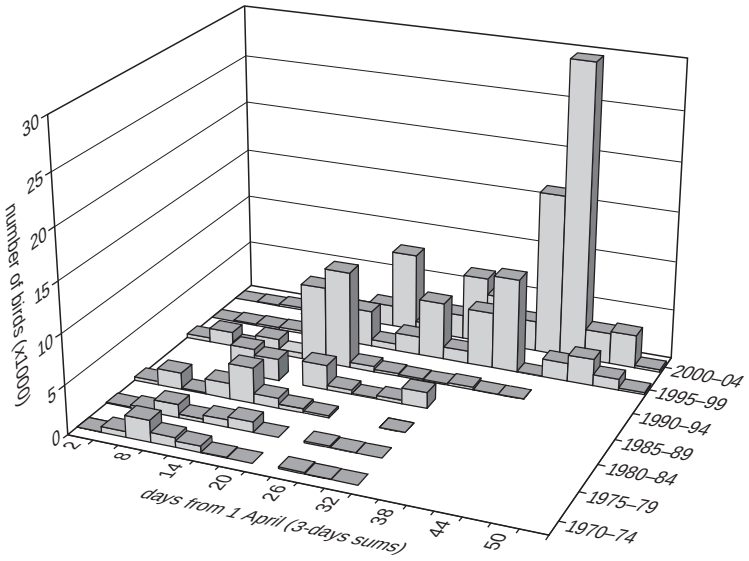

Figure 4.4. Development of spring migratory pattern of barnacle geese counted at Ottenby 1971-2004. Census data were first aggregated to three-day sums for each season (assigned to the central day of the interval) and then averaged over the periods indicated along the right axis (years with counts of < 5% of flyway population were discarded; see Fig. 4.2).

which was virtually identical to the peak dates of barnacle goose passage observed in southern Finland in these two years, i.e. 18 and 19 May. Some of the individuals had staged in the Baltic (having left the Wadden Sea as early as 23 March) according to the traditional strategy, others reached the White Sea virtually directly from the Wadden Sea (one individual covering 2250 km in two days, with hardly any opportunity for feeding along the way). These individuals, although nesting close together, did not winter or migrate together, but most converged on a staging site on the lower Dvina River near Archangelsk when they entered the White Sea (staging there about six days before moving on in short hops to the colony). As already shown for mass movements in Fig. 4.3, a delay in departure from the wintering grounds does not translate into a delayed departure from the Baltic staging sites. Instead, birds reduce their stay in the Baltic.

Both timing of geese observed during passage at Ottenby and of individually tracked birds from the same breeding colony imply that most geese prefer either an early (April) or a late (May) departure from the Wadden Sea but avoid the period in between (Figs 4.4 and 4.5). Thus, recently we encounter two major spring migratory strategies within one flyway population, which exhibit a difference of about one month in the timing of departure from the wintering grounds.

Although our sample is small, individual geese followed over several seasons were either consistently traditional 'Baltic stagers' or 'skipped' the Baltic following

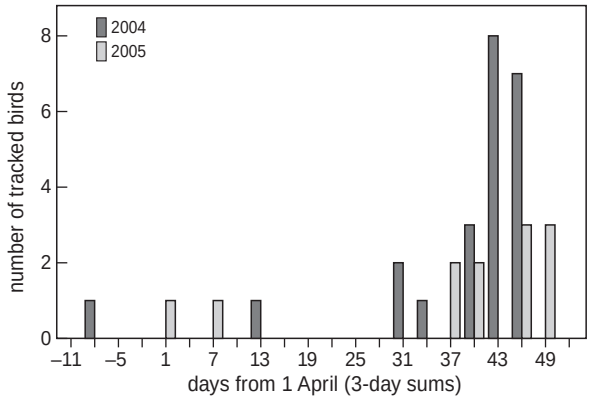

Figure 4.5. Timing of individual movements into the Baltic for birds tracked in 2004 (black bars, n = 23) and 2005 (grey bars, n = 12). Values were summed over three-day periods and assigned to the central day of the interval.

the new 'Wadden Sea stagers' strategy (Fig. 4.6, Table 4.1). However, switching may occur as was shown by one individual (M=W6) which adopted the new strategy in 2005. Because of the strong influence of a single bird in a relatively small sample we present results from repeatability analyses (Lessells and Boag 1987) for both the total sample and excluding bird M=W6 (Table 4.1). Despite the huge annual difference in departure date from the non-breeding grounds, the date of arrival at the breeding site (based on first observations in the colony) for this particular individual was remarkably similar in 2004 (7 June) and 2005 (8 June). The time window for arrival dates in the Baltic covered 58 days in these seven birds tracked over two years, whereas dates of departure from the Baltic fell into a period covering 13 days only (Fig. 4.6).

By-passing the baltic in view of optimal migration theory

The following exercise aims at estimating the differential energetic costs of the two migratory strategies and to evaluate conditions for an optimal spacing of migratory stopovers for a time-minimising capital breeder. We base our estimates on flight mechanical theory (Pennycuick 1975) and follow the principles outlined by Gudmundsson et al. (1991) and Alerstam & Hedenström (1998). The distance Y a bird can fly with a certain fuel load can be described by the range equation:

$$Y = c \cdot \left(1 - \frac{1}{\sqrt{1+f}}\right) \qquad \text{(eqn 1a)}$$

or

$$Y = \frac{c}{2} 1\mathrm{n}(1+f) \qquad \text{(eqn 1b)}$$

where f is defined as fuel load relative to the lean body mass of the bird and c is a

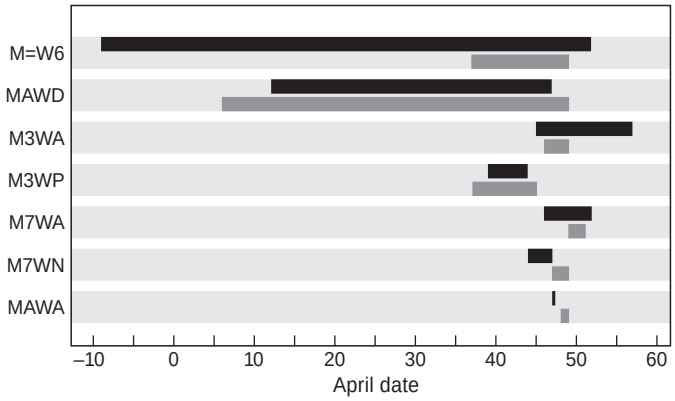

Figure 4.6. Timing and duration of staging in the Baltic for seven individuals tracked in two consecutive spring seasons, 2004 (black) and 2005 (grey bars). Labels given on the y-axis refer to individual colour-ring codes of the birds.

Table 4.1. Repeatabilities (r_i) of Baltic arrival, stopover duration and departure times of barnacle geese tracked in 2004-2005. Analyses were performed on the total sample of seven birds and again but excluding bird M=W6; see Fig. 4.6 for reference

	Total sample			Excluding bird M=W6		
Variable	r_i	F (df)	P	r_i	F (df)	P
Arrival Baltic	0.57	3.67 (6,7)	0.06	0.98	90.4 (5,6)	< 0.001
Stopover Baltic	0.59	3.82 (6,7)	0.05	0.93	29.1 (5,6)	< 0.001
Departure Baltic	0.39	2.27 (6,7)	0.15	0.47	2.79 (5,6)	0.12

constant (with same dimension as Y) that depends on factors such as bird morphology, muscle work efficiency, fuel composition and wind conditions. The difference between the two equations is whether one assumes that fuel load increases both induced and parasite drag of a flying bird (1a) or only the former component (1b) (see also Alerstam & Lindström (1990). The occurrence of parasite drag is expected due to an increased body frontal area when fuel is added (note the bulging abdomen of fat geese in flight). Therefore, we will proceed with equation (1a). We derived an empirical estimate for c from data reported by Madsen & Klaassen (2006) for pink-footed *Anser brachyrhynchus* geese flying between Denmark and Vesterålen (Norway). For this flight of 1410 km the authors estimated an average change in API (abdominal profile index) of 2.00 units (for both sexes), corresponding to 371 g and 394 g mass (fuel) loss in female and male geese, respectively (API-body mass relationship given in same paper). Fuel ratios were calculated by dividing these fuel losses by body mass upon arrival in Vesterålen (which was

also estimated from API, Madsen & Klaassen pers. comm.) yielding $f = 0.124$ (females, n = 18) and $f = 0.129$ (males, n = 17). Inserting these fuel ratios and the flight distance into equation (1a) gives $c_{females} = 24765$ km and $c_{males} = 23927$ km. We applied the rounded average of these values, $c = 24300$ km, as estimate for our further calculations.

Of fundamental importance here is to note that the potential flight distance is not a linear but a negatively accelerated function of fuel load, meaning that the marginal gain in flight distance diminishes with increasing fuel levels. Thus, overloading, which includes fuel in excess of what is needed to reach the next stopover site, must produce extra flight costs. Recent empirical information suggest possibly lower additive flight costs of carrying large fuel loads (Kvist et al. 2001). However, these results have not been confirmed so far and we consider it premature to adopt them here but realise that our quantitative predictions must be regarded as provisional. Rearranging equation (1a) to express fuel load as a function of potential flight distance $f(Y)$ gives:

$$f = \frac{1}{\left(1-\frac{Y}{c}\right)^2} - 1 \qquad \text{(eqn 2)}$$

From this equation we calculated the fuel loads needed to cover flight distances between stopovers for the two strategies, i.e. by-passing the Baltic or not, and for two scenarios depending on whether the next stopover beyond the Baltic is at the Dvina River or in the Kanin Peninsula (Fig.4.1, Table 4.2). The outcome of these calculations indicates that it costs approximately 8–10% extra fuel to pay the additional overload when the Baltic is skipped for fuelling en route to the arctic pre-breeding staging sites.

Overloading and by-passing can become optimal in time selected-migrants, when deposition rates at succeeding stopovers fall below that at the departure site. Thus, another avenue to explore the current phenomenon is to ask to what extent the fuelling rate in the Baltic must have dropped compared to the Wadden Sea to achieve an equal speed of migration by skipping the Baltic. We start again from the range equation and substitute f by $k{\cdot}t$, the product of the rate of fuel deposition (k) and time spent on deposition (t). Expressing equation (1a) now as a function of fuel deposition time $Y(t)$ a bird putting on fuel may be regarded as increasing its potential flight range with time. This instantaneous speed of migration (S) is found by differentiation yielding:

$$S = \frac{dY}{dt} = \frac{c}{2} \cdot k \cdot \frac{1}{(1+f)^{3/2}} \qquad \text{(eqn 3)}$$

By inserting $f(Y)$ from equation (2) into equation (3) S can be given as function of the potential flight range:

$$S = \frac{dY}{dt} = \frac{c}{2} \cdot k \cdot \left(1-\frac{Y}{c}\right)^3 \qquad \text{(eqn 4)}$$

The instantaneous speed of migration thus depends on the local fuel deposition rate but is devaluated by a factor (<1) reflecting the transport costs for the distance (*Y*) to the next stopover. With Y = 1000 km (i.e. the flight distance between Wadden Sea and Baltic) this deflation factor, $\left(1-\frac{Y}{c}\right)^3$, yields 0.88, indicating that at a deposition rate of 88% or higher in the Baltic compared to the Wadden Sea the birds should stopover there. This also means that if the deposition rate in the Baltic falls below 88% of that in the Wadden Sea, continued energy deposition at the latter site and a postponed departure from the Wadden Sea without stopover in the Baltic will be favoured.

Table 4.2. Flight distances (Y) and calculated fuel loads (f) using equation (2) and c = 24,300 km for migratory strategies depending on whether the Baltic is by-passed or not and whether the Dvina River or Kanin Peninsula is chosen as next fuelling site. The costs of by-passing the Baltic are expressed as additional fuel load and as percentage extra fuel needed relative to not by-passing the Baltic under the assumption that the birds leave for their next target site as soon as fuel loads permit to fly there. The geographical locations of the stopover sites are illustrated in Fig. 4.1

Flight	Y (km)	f (Y)	extra f	extra f (%)
Wadden Sea - Baltic	1000	0.09		
Baltic - Dvina	1470	0.13		
Baltic - Kanin	1910	0.18		
Wadden Sea - Dvina	2470	0.24	0.02	8.4
Wadden Sea - Kanin	2910	0.29	0.03	9.4

What are the Fitness Consequences of the New Strategy?

Since extra costs are involved in by-passing the Baltic staging site, the question arises if individuals following this strategy encounter certain fitness consequences. Our data on the reproductive output of tracked birds is too incomplete to be used for this purpose, as egg loss and nest desertion due to stochastic factors like predation, flooding events and human disturbance reduced the potential sample size substantially. However, we know the time of egg-laying for most of the birds (recall that for 'logger birds' incubation rhythm and start of egg-laying could be inferred from the light logger data, hence not necessitating direct observation of the breeding bird). We can use this parameter to assess potential penalties of the new strategy, because laying date is a good predictor of reproductive prospects in arctic geese. In our study colony 90% of fledged young derive from eggs laid over period of nine days (ch. 6 this thesis). Figure 4.7 shows individual case histories of departure date from the non-breeding ground and laying date collected over two seasons at the colony. It will be noted that the majority of birds following the new 'Wadden

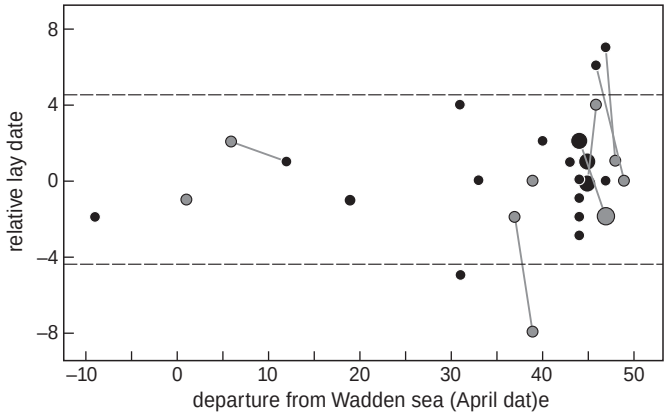

Figure 4.7. Lay date relative to the colony's median lay date versus departure date from the wintering grounds plotted for 21 females in 2004 (black dots) and 9 in 2005 (grey dots); size indicates sample size, small dot=1, large dot=2; lines connect individuals followed in both years. The two dashed lines include the time window of laid eggs producing 90% of all fledged young in the colony.

Sea stagers' strategy laid their eggs in the period conferring good prospects. Furthermore, no trend towards later laying as result of delayed departure can be identified (2004: n = 21, r = 0.21, NS; 2005: n = 9, r = –0.06, NS). Apparently, both strategies are successful with respect to laying eggs 'on time'.

Discussion

Both observations of departing geese in the north-eastern Wadden Sea and spring counts of geese passing over southern Sweden show that the majority of barnacle geese have delayed their departure from the non-breeding grounds by a full month. Moreover, this drastic shift evolved over a remarkably short period of five to ten years starting in the first half of the 1990s. Combining these findings with a stable peak migration date in Finland over the same period we conclude that Baltic stopover, formerly spanning a period of more than five weeks, has been reduced to less than seven days for a sizeable proportion of the flyway population.

Driving forces behind the emergence of a new migratory strategy

We propose that a capacity problem in the Baltic is the key for the emergence of the strategy of delayed departure from wintering grounds in the North Sea and reduced or omitted Baltic staging. Support for this claim comes from several sources. First, numbers of spring staging barnacle geese in Estonia followed the increase of the flyway population until mid 1990s but then levelled off and are decreasing over recent years (Fig. 4.2). Second, Van der Graaf et al. (2006b) compared nutrient bio-

mass (product of forage biomass and protein content) during spring staging in the Wadden Sea and on Gotland in 2003–2004 and noted higher values for the Wadden Sea site. High grazing pressure caused heavily reduced food availability, as was indicated by exclosure experiments. Confronted with increasing costs of competition (Moore et al. 2003) at the Baltic sites and constrained by the inaccessibility of sites further north along the route (which are still snow bound at that time) the geese concentrate on premigratory sites. It is important to note that most of the Wadden Sea sites where barnacle geese nowadays concentrate in spring have only come in use since the early 1990s, e.g. the Dollard estuary (Fig. 4.1) at the Dutch-German border (Aerts et al. 1996). In other words, the new 'delayed' strategy involves exploitation of new spring staging resources in the Wadden Sea as well as a change in timing.

The two strategies do not represent two ends of a continuum. Migrants appeared to prefer either an early (Baltic) strategy or a late (Wadden Sea) option while few movements occurred in between (Figs 4.4 and 4.5). Various factors may shape an individual's choice for the one or other strategy, such as individual competitive ability (Moore et al. 2003), strategy of parents or mate, experience and learning.

Further triggers of migratory schedules

In birds the timing of events through the annual cycle, including migration, has been shown to be regulated by the interaction of an internal circannual clock and environmental cues, of which daily photoperiod is the most important one (Gwinner 1996). Studying free-ranging Bewick's Swans Rees (1989) suggested individual response thresholds to photoperiod triggering spring departure. However, the strong and rapid shift in departure time of (individual) barnacle geese (see next section) does not support this hypothesis. We expect photoperiod as Zeitgeber to be primarily relevant for the timing of physiological responses accompanying migratory preparation, mainly related to the deposition of body stores (Bairlein and Gwinner 1994), rather than triggering actual migration (but see Helm and Gwinner 2005).

Recently, shifts in migration patterns of many bird species have been reported in NW Europe, and credible relationships with climatic variables such as temperature and the North Atlantic Oscillation (NAO) have been established (e.g. Møller et al. 2004; Stervander et al. 2005). Among waterfowl studies Pistorius et al. (2006) suggested that increasingly warmer spring temperatures in The Netherlands may have driven temporal changes in arrival and nesting of greylag geese *Anser anser* breeding on the Helgeland coast in central Norway. This population uses Dutch spring staging sites on their migration from Spanish wintering grounds. Arrival and nesting of the geese in Norway has been advanced by more than two weeks over the past three decades.

The seasonal progress of vegetation development in temperate regions, notably the onset of leaf growth, is closely related to growing degree days (GDD), i.e. the sum of daily mean temperatures above a defined threshold accumulated over a certain period (Botta et al. 2000). Using 'onset of spring' (defined as a GDD value of

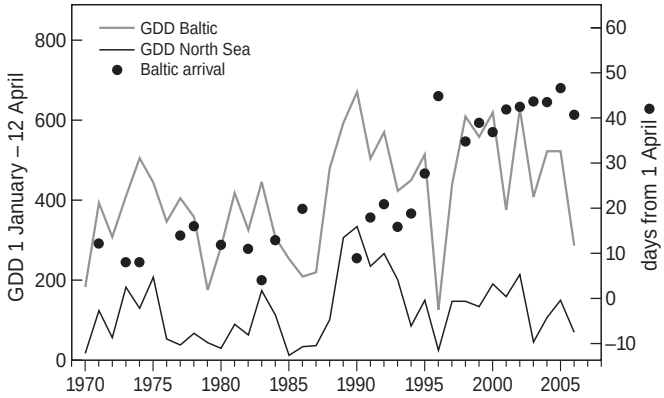

Figure 4.8. Annual Growing Degree Days (GDD) accumulated over 1 January–12 April (left y-axis) at a Baltic and Dutch staging site, denoted by the lower and upper line, respectively. Linear regression analyses revealed a significant increase of 5.0 GDD/year over the study period for the Dutch site ($F_{1,35} = 6.1$, $P = 0.02$) but not for the Baltic site ($F_{1,35} = 2.3$, $P = 0.14$). Also shown are median arrival dates of barnacle geese in the Baltic as presented in Fig. 4.3.

180 accumulated above a threshold of 0°C) Van Eerden et al. (2005) compiled data on the timing of spring migration of barnacle geese from the Russian flyway population along the whole route and concluded that their measure of onset of spring was in close accord with the timing of geese (observations 1990–2003). We analysed our data on the timing of yearly mass movements of barnacle geese into the Baltic together with annual GDD values (see methods) at a Baltic and Dutch staging site (Fig. 4.8). Although GDD measured at the two sites correlate ($r = 0.80$, $P < 0.001$, n = 37), springs were substantially warmer since 1990 in the Dutch site compared to the Baltic. The Dutch site also showed a significant increase in GDD over the total study period, whereas the slight increase in Baltic GDD was insignificant (Fig. 4.8). These findings are supported by the regional pattern of NDVI (Normalized Difference Vegetation Index) derived changes in onset of spring observed by Høgda et al. (2001). For the period 1982–1998 these authors report an advance in the onset of spring of four or more weeks for most of the Wadden Sea area but only about two weeks for the eastern Baltic.

Using regression analysis we further investigated the effects of GDD, year and year2 on barnacle goose median arrival date in the Baltic for the period before 1990 and for the period from 1990 onwards (GDD measured at the Dutch and Baltic site were each separately tested together with year effects). We analysed these two periods separately, because we were interested in comparing the influence of GDD on migratory timing before and after birds started to delay their departure from the non-breeding grounds. Higher (lower) GDD measured at both sites triggered to a significant extent advanced (delayed) arrival in the Baltic during the first period before 1990 (n = 10) while there was no effect of year ($F_{1,9}$ $GDD_{North\ Sea} = 11.14$,

$P < 0.05$, $r^2 = 0.58$; $F_{1,9}$ $GDD_{Baltic} = 12.22$, $P < 0.01$, $r^2 = 0.60$). However, in the recent period from 1990 onwards (n = 16) considerably more variation was explained by a quadratic year effect (see Fig. 4.3 for statistical tests and calculated parameters). At the same time, the effect of GDD disappeared ($F_{1,15}$ $GDD_{North\ Sea} = 2.64$, NS; $F_{1,15}$ $GDD_{Baltic} = 0.75$, NS). Alternatively, we calculated GDD values accumulated until the actual median departure date for each year revealing small fluctuations around 366 ± 68 (mean ± SD, n = 10) and 94 ± 49 at the North Sea and Baltic site, respectively, before 1990. Thereafter GDD increased considerably up to average values of 803 ± 139 (North Sea) and 369 ± 87 (Baltic site) for the years 2000-2006 (n = 7).

Thus, our findings refine the conclusion of Van Eerden et al. (2005, see above) and suggest a temporal change in the relationship between seasonal development of forage plants (GDD used as a proxy) and timing of migration from the Wadden Sea. We conclude that seasonal progress in vegetation development has a potential effect on migratory timing in barnacle geese. However, GDD cannot explain the observed delay in departure from the wintering grounds followed by an increasing share of the population. The modulating effect of spring development on departure decisions has recently been overruled by other factors, of which we regard the capacity problem in the Baltic as the dominant one.

Consistency in individual migratory behaviour

The barnacle goose is a long-lived species. Ebbinge et al. (1991) estimated a mean annual survival rate of adult birds belonging to the 'Russian flyway population' of 90% corresponding to a mean life expectancy of nine years (Seber 1982) and life spans of more than 20 years have been frequently recorded for birds from this population (Ebbinge pers. comm.). Given the short time span over which the shift in migratory timing in the population occurred, it is evident that this process must have involved individually altered behaviour. This conclusion is reinforced by the observation of one tracked individual departing from the North Sea 44 days later in 2005 compared to the previous year. Nevertheless, the overall pattern hints at individual consistency after the adoption of a new migratory schedule.

Individual consistency in annual bird migratory schedules has been proven for a number of species and populations. However, most of these studies dealt with timing from or to a single site (e.g. Rees 1989; Møller 2001; Forstmeier 2002; Gunnarsson et al. 2006; Battley 2006). Only few studies included more than one site (Bêty et al. 2004) or the entire migratory route (Berthold et al. 2002; Berthold et al. 2004; Phillips et al. 2005; Alerstam et al. 2006). The osprey *Pandion haliaetus* study of Alerstam et al. (2006) revealed that individual consistency (repeatability as high as $r_i = 0.81$) in timing observed at one site (e.g. departure site) does not necessarily persist throughout the entire migratory route. Temporal patterns at subsequent sites (e.g. arrival site) can differ and furthermore may vary between homeward and outward migration. Bêty et al. (2004) reported a site dependence of annual consistency for female greater snow geese *Anser caerulescens atlanticus* which showed relatively high individual consistency in the arrival date at the breeding site

on Bylot island (r_i = 0.42) but not in the departure date from a major staging site at the St. Lawrence river 3,000 km away. For our barnacle geese we found consistent patterns for the timing of arrival and stopover duration in the Baltic (Table 4.1). Increasingly tighter migration schedules as birds get closer to their breeding grounds, as indicated here for geese by their first two major leaps (to and from the Baltic), may be common among long-distance migrants (Battley et al. 2004; Gunnarsson et al. 2006).

Flexibility of migratory schedules

Whether the recently observed rapid advance of spring arrival of long-distance passerine migrants throughout Europe reflects an evolutionary response or a phenotypic reaction to changed environmental conditions is matter of current debate (Both 2007; Jonzén et al. 2007). For the barnacle goose most of the flexibility in migratory schedule must be attributed to phenotypic plasticity. Most barnacle geese do not start breeding before three years of age and breeding success is usually low during the first attempts (Black et al. 2007). The observed response was too rapid to be produced by natural selection, even when strongly directional (note also that 'traditional' schedules seemed not per se to incur fitness penalties). Furthermore, in geese migratory routes are transmitted culturally by the family, where young benefit from the experience of their parents, which helps them to optimise their own future decisions (Sutherland 1998). The barnacle goose is a highly sociable species breeding in colonies and living in flocks for the rest of the year. Scheduling of events is virtually always a sociable process in this species and social information transfer likely boosts speed and extent of adjustments to new environmental conditions (Helm et al. 2006). Cultural transmission need not be restricted to parent-offspring relationships. Social learning and communal decisions can involve more members of the flock and lead to concerted group behaviour further enhancing speed of phenotypic reactions (Galef and Heyes 2004; Couzin et al. 2005; Conradt and Roper 2005). Moreover, learning from their own experience represents effective means for optimal adjustments. If short-living blue tits *Cyanistes caeruleus* are able to exploit previous experience to adjust seasonal schedules a year later (Grieco et al. 2002), there is reason to assume ample scope for such capacity in long-lived geese. Indeed, Madsen (2001) showed how pink-footed geese explored alternative spring migratory strategies and switched among them depending on the repercussions on breeding success. For the same species Klaassen and co-workers (2006) highlighted the importance of learning to cope with rapidly altered conditions along the spring flyway. Their modelling exercises predicted dramatic differences in fitness consequences between omniscient and naïve geese. The authors emphasise that time is a crucial factor to allow the birds to experience, learn and readjust migratory strategies in an adaptive fashion.

Costs and consequences of the new strategy

In our attempt to quantify costs of the new strategy we classified it as essentially by-passing the Baltic. It should be noted that the majority of birds included at least

a short visit in the Baltic region, mainly to Estonian sites in the eastern Baltic (Eichhorn et al. 2006). However, settling costs and heavy food depletion at that time (Van der Graaf et al. 2006b) will make significant fuel gain during such short stopover periods unlikely. The results indicate that the marginally higher costs of extra fuel load needed to by-pass the Baltic must be compensated for by overall higher fuel deposition rates in the 'Wadden Sea stagers' if they are to arrive with same reserves and at the same time in the Arctic as the 'Baltic stagers'. The geese should skip the Baltic whenever the energy deposition rate falls below 88% of the Wadden Sea value.

Can this by-passing behaviour be explained by a general latitudinal gradient in stopover site quality along the route? Gudmundsson et al. (1991) hypothesised for arctic waders a decline in deposition rates when moving north, because spring development at higher latitudes lags behind that at more southern latitudes, and from this perspective overloads would be favoured. For arctic geese the situation seems, however, to be largely the opposite. Here gain rates usually accelerate along the spring migratory route (Prop 2004; Madsen and Klaassen 2006; Klaassen et al. 2006). Both food quality (in terms of nutrient content and digestibility) and available feeding time are crucial determinants for the rate of nutrient deposition. Growing grass shows a higher digestibility and concentration of nutrients, and while moving northwards, these herbivorous birds can take advantage of a 'green wave' generated by spring growth at subsequent stopovers (Drent et al. 1978; Owen 1980). Additionally, with latitude they encounter increasing daylength which extends potential feeding time. Only towards the end of spring migration, when at or very close to their destination, geese are forced to get ahead of the green wave in order to match hatching of offspring with the local crest in food quality. Theoretically, for 'Baltic stagers' one would expect not only reduced flight costs but also potentially higher fuel gain rates. That these potential benefits were indeed realised in former times can be inferred from mean body masses of spring staging geese recorded in the Wadden Sea and on Gotland in the period 1979-1989 (Ebbinge et al. 1991). Geese on Gotland showed impressive mass gains after intensive use of this Baltic stopover in those days.

A crucial question when dealing with a strongly expanding population such as our study species is whether some of the birds are being forced into less favourable habitats, i.e. entailing a heightened risk of mortality and/or decreased reproductive success. The Icelandic population of the black-tailed godwit *Limosa limosa islandica* wintering in Britain has increased fourfold since the 1970s, and Gill et al. (2001) demonstrated that this coincided with expansion into heretofore unused estuaries. Godwits wintering in these new sites suffered both a higher mortality and arrived later on the breeding grounds in Iceland presumably leading to a lower breeding success than individuals utilizing the traditional estuaries. Subsequently Gunnarsson et al. (2005) showed that in Iceland the population expansion was associated with an overflow into new breeding habitats conferring lower breeding success, hence this godwit population can be said to experience a double buffer effect (sensu Kluyver and Tinbergen 1953). Since our tracking of barnacle geese was undertaken

primarily with breeding females caught at a specific colony (and not a cross-section of the wintering population as in the godwit) the existence of a buffer effect in our study system remains an open question.

We are aware that subtle effects on survival and reproductive success are associated with changing stop-over patterns during spring migration in the pink-footed goose of the Svalbard population (Madsen 2001) despite its relatively modest size. However, for the Russian barnacle goose population we have so far found no tangible signs of a buffer effect associated with the saturation of the Baltic sites thus penalising the recently evolved alternative strategy of delayed departure from the Wadden Sea. Timing of egg-laying (a strong predictor of potential breeding success) was the same for 'Wadden Sea-stagers' and 'Baltic-stagers', and while the proportion of 'Wadden Sea-stagers' increased, the overall population showed a hitherto unbroken geometric growth. Apparently, by their large-scale change in site and habitat use the geese have managed to spread optimally over the total of resources available to them in the North Sea-Baltic region during spring thereby escaping negative effects of density dependence. Van Eerden et al. (2005) have argued convincingly that this was largely facilitated by the acquisition of new resources in form of improved grassland, where forage quality is enhanced due to intensive agricultural fertilization during the past 20 years. At these agricultural sites the geese have yet to face a depletion problem but cope successfully with the very productive vegetation. Aggregation and extended grazing of the geese helps to maintain and prolong the profitable phase of the vegetation in the Wadden Sea in spring (Bos et al. 2004; Van der Graaf et al. 2005).

Mortality risk due to predation is another factor determining site quality and may play an important role in the development of migratory strategies (Alerstam and Lindström 1990; Lank et al. 2003). Barnacle geese experience predation risk from white-tailed eagle *Haliaeetus albicilla*. This raptor enjoyed a dramatic increase in numbers in the Baltic over the past decades, in contrast to the Wadden Sea where the species is still uncommon. The Estonian white-tailed eagle population recovered from a low of ca. 16 pairs in 1970s and numbered 110–120 pairs in early 2000s (Randla 1976; Elts et al. 2003). On northern Öland eagles started to breed again in 1994 and reside there now with about ten pairs (own obs.). Beside the risk of being predated the geese suffer enhanced energy costs and a loss of feeding time due to eagles' hunting efforts. Such additional costs of a relative change in quality of Baltic and Wadden Sea staging sites may have further facilitated the observed change in goose migratory strategy.

No fitness penalties for birds delaying their departure from the Wadden Sea and subsequently 'skipping' the Baltic were revealed by the timing of egg-laying (Fig. 4.7). Furthermore, no signs of retarded growth of the flyway population can be noted so far (Fig. 4.2). Apparently, the enhanced gain rates compensate the 'Wadden Sea stagers' for the loss of an intermediate fuelling site and probably have facilitated the growth of the flyway population in combination with reduced mortality through enhanced protection (Ebbinge 1991). Finally, conditions encountered after the Baltic stopover may have improved to compensate for the loss of the Baltic fuelling site.

The 1990s marked a period of substantial expansion of barnacle goose breeding area towards south-west along the Russian coast (Syroechkovsky 1995). Geese may have benefited from breeding at these new sites by more benign climatic conditions allowing higher plant productivity over a longer season and by a shortened migratory distance.

The remarkable phenotypic plasticity demonstrated by this species will enhance its ability to cope with current and future environmental changes including climate change.

Acknowledgements

We thank all collaborators of the Dutch-Russian expeditions to Tobseda, and Konstantin Litvin in particular for his unflagging efforts at capturing geese. Mennobart van Eerden played an important role in the organization of these expeditions. Support by the Institute of Biology in Syktyvkar, by the administrations of the Nenets Autonomous District and the State Nature reserve Nenetskiy, and by the Russian Hunters Association is gratefully acknowledged. Petteri Tolvanen and Anders Hedenström helped to retrieve data on goose passage over Finland and Ottenby, respectively. GLS loggers were developed at the British Antarctic Survey and we want to acknowledge the technical skills of Vsevolod Afanasyev in particular. Jochim Lage gave helpful advice during the process of light-level data analysis. Financial assistance came from the Dutch Institute RIZA, the Schure-Beijerink-Popping Fonds, the University of Groningen, the Deutsche Forschungsgemeinschaft and the Netherlands Arctic Programme of NWO. GE was supported by ESF travel grants and scholarships from the 'Marianne und Dr. Fritz Walter-Fischer Stiftung', Germany, and the 'Ubbo Emmius Programme' of Groningen University.

Chapter 5

Migratory connectivity in Arctic geese: spring stopovers are the weak links in meeting targets for breeding

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Journal of Ornithology (2007) 148: S501–S514

Abstract

Linking spring migratory itineraries of individual Arctic-breeding geese to their eventual breeding success has provided evidence that accumulation of body stores (protein, fat) at stop-over sites is crucial. We show that this is because geese nesting in the Arctic depend at least in part on these stores for synthesis of eggs and supporting incubation (for the female a phase of starvation). Estimates of the body stores needed for successful reproduction (eggs + incubation) in relation to measured rates of accumulation of these stores make clear that meeting the demands solely by feeding at the breeding grounds is not an option for geese. The time constraint does not allow this, because early laying is a necessity in the Arctic to ensure survival of the progeny. Although the parents can exploit the early spring growth along the flyway, they get ahead of the wave of growth when they arrive on the breeding site and hence the parental time-table can only be met by drawing on body stores. Results from tracking studies in six goose species underline the conclusion that egg formation commences along the flyway before arrival at the nesting colony. In some cases signatures of stable isotopes in egg components and parental body tissues in relation to the signature in forage plants support the notion of a mixed endogenous/exogenous origin. The close match between migratory timing and the spring flush of plant foods makes geese particularly vulnerable to the impact of climate change. There is an increasing mismatch along the NE Atlantic Flyway, where a warming trend in NW Europe conflicts with stable or even cooling trends in the Arctic target areas.

Introduction

Migratory birds face the challenge of producing a clutch as soon as possible after arrival on the breeding grounds, since the prospects for progeny decline rapidly with advancing date (Sedinger and Raveling 1986; Sedinger and Flint 1991; Lepage et al. 1998; Prop et al. 2003; Bêty et al. 2003; 2004). Especially in demanding environments still in the grip of winter the nesting female will face a shortage of foraging opportunities locally and may depend instead on nutrients garnered elsewhere along the flyway and sequestered in the body (notably stores of fat and protein) in order to meet her time schedule. Birds that follow this strategy of flying in materials for forming the eggs and supporting incubation have been termed 'capital breeders' in distinction to 'interest breeders' relying on nutrient sources collected locally on the breeding grounds following the rule 'pay as you go' (Drent and Daan 1980). Although these terms have been widely accepted, strict dichotomies are rarely valid in biology. Currently, the focus is on the quantification of the contributions from body stores on the one hand and nutrients garnered locally on the other, as we have come to realise that many (most?) bird species in fact follow a mixed strategy. In this paper we return to Arctic-nesting geese that provided one of the classic examples of capital breeding (reviewed by Meijer and Drent 1999; and Klaassen 2003) and will consider new sources of information that clarify the situation. Figure 5.1 depicts the conventional terminology in distinguishing nutrient sources for avian reproduction. We consider the distinction between the use of 'endogenous' and 'exogenous' nutrient sources as equivalent to the 'capital' and

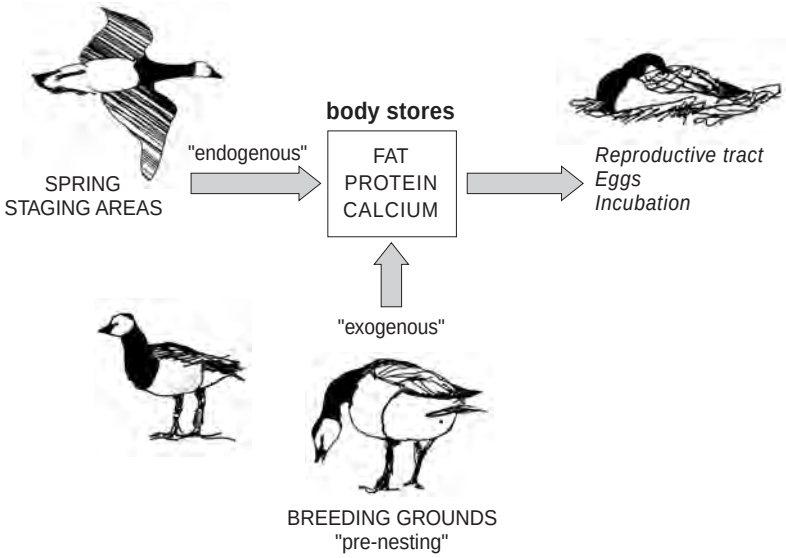

Figure 5.1. Diagram elucidating distinction between use of endogenous versus exogenous nutrient sources for breeding in Arctic nesting geese. Note that incubation is a phase of starvation.

'interest' breeding strategies. Note that not only must we investigate the nutrient sources for hypertrophy of the reproductive tract and for synthesis of the eggs, but also must consider the balance sheet for incubation. In waterfowl, with very few exceptions incubation is carried out solely by the female (Afton and Paulus 1992; Bowler 2005). Attentiveness is generally very high (usually above 90% of the 24 hr) and this preoccupation with the nest severely limits the time free for foraging. Collecting food is a time-consuming process in herbivorous species such as geese, so balancing the daily energy budget during incubation is potentially a problem for the female. Houston et al. (2007) have recently proposed a generalised model for female reproductive strategies, distinguishing capital from income breeding. Although formulated primarily for mammalian life histories, when applied to birds their model is not restricted to production of eggs alone, but includes transfer of maternal resources during incubation, conforming to our usage here.

Posing the question where migrant birds obtain the nutrients needed for reproduction ties in with the study of timing along the spring flyway. For waders and waterfowl returning to their Arctic breeding stations migration generally proceeds in relatively long leaps. Staging sites tend to be geographically confined and Alerstam et al. (1986) have pointed to the paradox that besides functioning as *spring-boards*, spring staging sites may potentially become *bottle-necks* whenever forage is in short supply. Alerstam and co-authors considered especially the role of competition, and in addition vagaries of the weather can lock up resources unexpectedly in ice and snow. Herbivorous migrants such as geese move up a climatological gradient, taking advantage of the spring flush of grass at each stopping place (Owen 1980). The growing grass has a higher digestibility and Drent et al. (1978) suggested that Barnacle Geese were riding the crests of digestibility waves as they moved during the course of the year, and termed it "the Green Wave hypothesis". For Arctic geese, the window of opportunity for laying eggs with good prospects is often as short as a single week in the year. This finding leads to the proposition that the geese at their destination are forced to get ahead of the green wave generated by spring growth in order to lay on time, underlining their reliance on capital breeding. Obviously climate change, especially if uneven along the flyway, is a threat to the reliability of this gradient in spring growth the migrants depend on.

Field approaches

The classical approach to partitioning the nutrient sources used for breeding in geese has relied on (1) collecting specimens at intervals during the reproductive cycle and subsequently undertaking carcass analysis to follow changes from arrival, through egg-laying to incubation. Quantifying these changes allows reconstruction of the allocation of body stores for breeding (reviewed by Alisauskas and Ankney 1992a). The refinement of analysis techniques for stable isotopes has opened new avenues, as (2) the isotope signatures of egg components and body tissues reflect the signatures in the foods utilised for synthesis (reviewed in Hobson 2003; 2006).

Especially where sharp switches in diet occur during migration (for example moving from marine to terrestrial foods as is typical for many waders and some geese) analysis of egg components and body tissues in relation to the candidate substrates can lead to clear-cut results (Klaassen et al. 2001; Schmutz et al. 2006). During the incubation phase when the female is a prisoner on the nest several indirect techniques have been employed to measure energetic costs. These include (3) periodic weighing of the sitting female using balances inserted beneath the nest (Spaans et al. 1999; Spaans et al. 2007) and (4) repeated capture of the sitting female to ascertain total body stores of protein and fat by employing isotope enrichment (Groscolas et al. 1991; Speakman et al. 2001). This method relies on releasing isotopically labelled water molecules into the body and after equilibration determining isotope concentrations in the blood as a proxy for the body water. Since protein in the body is associated with a remarkably stable proportion of water, whereas fat is nearly free of water, the isotope values in conjunction with total body mass can be used to partition body stores into fat and protein compartments. In some species it has been possible to measure gaseous exchange (5) by lowering a hood connected by pumps to analytical equipment over the sitting bird (Parker and Holm 1990; Gabrielsen et al. 1991). These measurements allow estimation of whole animal metabolism and can be compared to determinations on resting values from the same species collected by standard laboratory procedures. Finally (6) the doubly labelled water technique (DLW) has sometimes been employed to measure total energy expenditure of incubating parents (Piersma et al. 2003) and is a method of great potential (capture and recapture is a prerequisite).

These hands-on techniques can nowadays be supplemented by detailed information on the location of females in the period of egg formation. For most avian species the period of explosive follicle enlargement when the egg is formed is known accurately or can be closely approximated and can be counted back from the observed laying date (Carey 1996b). In special circumstances direct observation of marked birds along the flyway can be related to laying dates of the same individuals (Prop et al. 2003). Tracking using miniature radios or satellite (PTT) transmitters has elucidated the whereabouts of individual geese with known laying dates during the critical pre-laying phase (Eichhorn 2005; Hupp et al. 2006b). The extensive comparative studies on Canada Geese *Branta canadensis* evaluated by Hupp et al. (2003; 2006a) as well as on Blue winged Teal *Anas discors* by Garrettson and Rohwer (1998) and Garrettson et al. (2000) clearly show that wherever possible abdominally implanted devices should be employed, as this technique has least adverse effects on behaviour, reproduction, survival and migratory timing.

Results

1. Energy requirement for incubation in waterfowl

Pooling data from a variety of waterfowl species justifies the simplification that the metabolic cost to the sitting female during steady (i.e. uninterrupted) incubation is

Table 5.1. Spring connectivity in Arctic geese: import of body stores to the breeding area

Species	Spring staging site	Distance to breeding goal	Evidence	Authority
Greater Snow Goose	St Lawrence (Quebec)	3000 km	stable isotope signatures	Gauthier et al. 2003
Anser caerulescens atlanticus			individual tracking	Bêty et al. 2004
Lesser Snow Goose 1	Corn belt (Manitoba)	1000 km	stable isotope signatures	Klaassen et al. 2006b
Anser c. caerulescens				
Lesser Snow Goose 2	Cook Inlet Alaska	1050 km	arrival phenology	Krechmar and Kondratyev 2006
Greater White-fronted Goose 1	Iceland	1400 km	individual tracking	Fox et al. 2003
Anser albifrons			Ova in birds collected in Greenland	Fox pers. comm.
Greater White-fronted Goose 2	Hokkaido	3175 km	individual tracking (n=1)	Takekawa et al. 2000
Pink-footed Goose	Vesterålen (Norway)	1100 km	individual tracking	Glahder et al. 2006
Anser brachyrhynchus				
Barnacle Goose 1	Helgeland (Norway)	1100 km	individual tracking	http://www.wwt.org.uk/barnacle/
Branta leucopsis			coordinated sightings	Prop et al. 2003; Hübner 2006
Barnacle Goose 2	Wadden Sea	3000 km	individual tracking	Eichhorn et al. 2006
Light-bellied Brent Goose	Denmark	3500 km	individual tracking	Clausen et al. 2003
Branta bernicla hrota				
Dark-bellied Brent Goose	Wadden Sea		individual tracking	Green et al. 2002
Branta b. bernicla			coordinated sightings	Spaans et al. 2007
Emperor Goose *Chen canagica*	Alaskan Peninsula	600–700 km	stable isotope signatures	Schmutz et al. 2006

closely related to resting metabolic rate. Daily energetic expenditure can thus reliably be predicted from body mass at least in the range above 1 kg (Fig. 5.2, methods and references indicated in key). To convert mass loss (g/day) to energy (kJ/day) we have employed the value of 24 kJ per g body mass obtained by Le Maho et al. (1981) from experimental work on fasting geese (closely similar to conversion factors in four other non-passerines including the Common Eider *Somateria mollissima*, see Spaans 2007 and Boismenu et al. 1992). The most notable feature of this compilation is that all values lie below the predicted RMR (Resting Metabolic Rate) according to the most recent predictive allometric body mass-relationship for swans and geese of Miller and Eadie (2006). It should be pointed out however that using a multi-species relationship for predicting RMR for individuals with large fat stores in the body (such as our incubating females) is bound to lead to overestimation as fat is a metabolically inert tissue. In any case energetic expenditure during quiet incubation is apparently kept to a minimum. Also shown is the contribution of body stores in covering these costs, and it will be noted that most of these uniparental incubators follow a mixed strategy supplementing foraging inputs during nest absences by drawing on body stores of fat and protein. Two species qualify as 'pure capital incubators': the Common Eider and White-fronted Goose *Anser albifrons* (Spaans et al. 1999, not shown in Fig. 5.2) which did not feed throughout. Now we face the question of the origin of these body stores supporting nearly a month of fasting. An approximation of the time course required for building up these fuel stores in the body can be derived from information on maximum fuel deposition rates in migrating birds.

Lindström (2003) compiled a massive data set on mean daily body mass increments from populations as well as individuals of migratory birds sampled in the field at intervals during episodes of rapid fuelling (48 populations and 39 individuals respectively, covering 59 species in all). He found that maximum daily fuel deposition rates expressed as percentage increment in relation to lean body mass did not depend on avian group (passerine or non-passerine) but depended strongly on body mass (BM, in kg) according to the formula $1.16\ BM^{-0.35}$ (populations) and $2.17\ BM^{-0.34}$ (individuals). Relative daily fuel deposition rates thus decline with increasing body mass: heavier species require more time to achieve the same proportional increase. The waterfowl species in our data set on incubation energetics (Fig. 5.2) are best represented in the 'population' set in Lindström (2003), and we will use that relationship in further calculations. Accepting the simplification that the mass increments measured in Lindström's data set when migrants are 'fattening' is energetically similar (kJ/g) to the body stores drawn upon during incubation, we can carry out a first approximation of the time required (in days) to build the stores sequestered by the female before undertaking incubation.

For the two goose species where contribution from the body stores during incubation has been estimated, empirical estimates are available on fuelling rates (Lindström 2003 and our own data). Females would require 10–12 days to accumulate the stores consumed during incubation (assuming full allocation towards body reserves during fuelling, i.e. no competing needs such as egg formation). For the

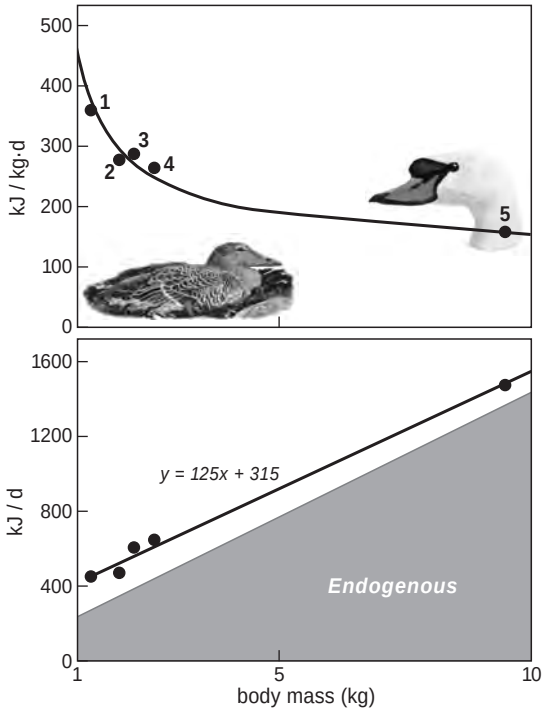

Figure 5.2. Daily energetic costs during steady incubation in relation to lean body mass in waterfowl depicted as energetic intensity (kJ/kg/d) upper panel and total costs (kJ/d) below. The formula y (in kJ) = 125 x (body mass in g) + 315 estimates daily costs (r^2=0.99). 1=*Branta bernicla bernicla* (Spaans et al. 2007), 2=*Somateria mollissima* (Parker and Holm 1990), 3=*Somateria mollissima* (Gabrielsen 1991), 4=*Anser caerulescens* (Ankney in Afton and Paulus 1992), 5=*Cygnus olor* (Ubels et al. unpubl. ms). The proportion of the daily requirement met from body stores is shown diagrammatically by the shaded area "endogenous".

Common Eider we have approximated the fuelling rate from Lindström's formula (13 g/day) and on this basis accumulating the body stores needed to support full incubation (24.2 days at 20 g/day, see Parker and Holm 1990; Gabrielsen et al. 1991) would require 38 days (again a minimal estimate assuming no competing requirements). To typify Arctic breeding swans calculations can be provided for Bewick's Swan (LBM and incubation period from Reese 2006). Assuming that 90% of the energetic requirement (from the formula in Fig. 5.2) is withdrawn from the body then accumulating the necessary body stores would take 35 days (daily fuelling rate from Lindström's 2003 formula works out at 0.7 % at the LBM of 4.1 kg). This exercise demonstrates the extended time span female waterfowl need to accumulate the body stores essential to complete incubation successfully. Field observations confirm that females feed intensively before laying, but the requirements for synthesis of ovaries and eggs will compete with accumulation of body

stores for later use. Energy deposition to pay for incubation will thus extend over more than the 10-38 days we have computed here. Precise information on arrival times in the breeding colonies can serve to put these minimal fuelling times in perspective, to help answer the question where fuelling for incubation occurs.

2. Arrival dates in relation to egg laying

Precise intervals between arrival at the colony and laying of the first egg have been obtained in several goose species breeding in the Arctic. Hupp et al. (2006b) tracked individual Emperor Geese *Chen canagica* returning to the nesting colony on the Yukon-Kuskokwim Delta in Alaska. In two seasons with early snow melt, the median interval between arrival and first egg was 11 days (mean 10 days, n=15) and slightly longer in a season of late snow melt (median 15 days, n=20). In the early seasons some individuals arrived only 4 days before laying, and Hupp et al. (2006b) conclude that in these years more than 50% of the geese likely initiated rapid follicle growth prior to migrating from the spring staging sites in the Alaskan Peninsula (600-700 km away). According to the tracking data the geese spent 30-40 days at these spring fuelling stations. The geese utilise marine foods at that time (especially the shellfish *Macoma*) and switch to terrestrial foods when they reach the breeding grounds. This dietary switch forms a convenient time marker for employing stable isotopes, since the signatures of the food types are readily distinguished. On this basis Schmutz et al. (2006) were able to confirm that endogenous stores available to the Emperor Goose during incubation indeed derived from marine environments (presumably the intertidal habitats in the Alaskan Peninsula). According to isotope analysis nutrients in the egg were a mix of terrestrial and intertidal sources, conforming to the time patterns of movements of the geese revealed by the tracking studies.

Eichhorn (2005) and Eichhorn et al. (2006) employed satellite tracking and Global Location System (GLS) loggers in Barnacle Geese *Branta leucopsis* at a breeding colony in Arctic Russia where laying dates of these individuals could be determined from direct observation and found that the 12-day phase of rapid follicular development was spread over a number of localities along the Arctic coast within 700 km and hence only a few hours flying time of the nest site (Fig. 5.3 and 5.4). Most geese arrived in the colony 4–6 days before laying the first egg, but one individual laid the very day she arrived. These findings imply a mixed strategy of using endogenous and exogenous nutrient sources for egg formation, and in view of the time scale of building up the fat stores required to sustain incubation (see above) this mixed strategy applies equally to the incubation phase. Prop et al. (2003) studied spring migration in the Spitsbergen breeding population of the same species, relying on intensive observation of individually ringed birds. The interval between departure from the last 'spring-board' in northern Norway and settling in the colony on Spitsbergen (1100 km away) averaged 19–20 days for 14 successful females (respectively in late and early seasons). During this interval the geese obtain some food in snow free patches on Spitsbergen, notably SW facing mountain slopes where snowmelt is early. At one such site intensive observation of ringed

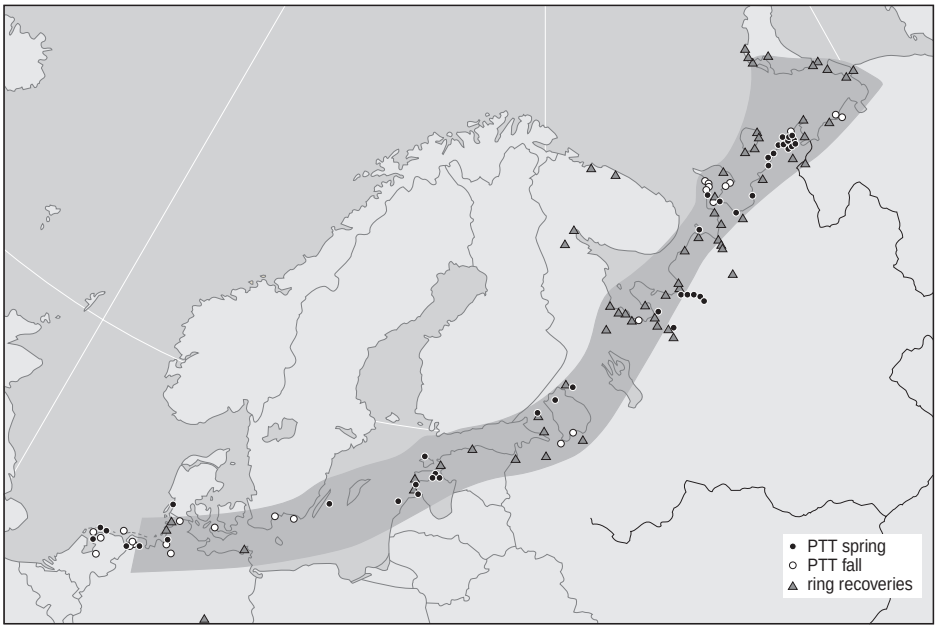

Figure 5.3. Migratory flyway of the Russian population of the Barnacle Goose, determined from ring recoveries (1965-2003) and results from satellite tracking (autumn 2004, spring 2005; from Eichhorn 2005).

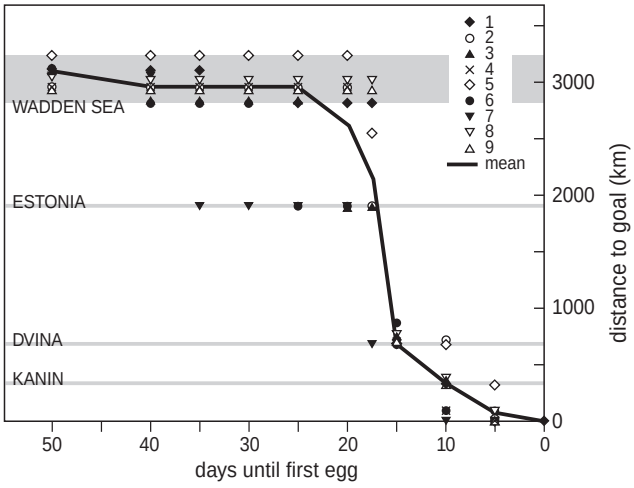

Figure 5.4. Progress towards nesting colony (in kilometres) of nine satellite-tagged Barnacle Geese in spring 2005, plotted relative to the day of laying the first egg. The Wadden Sea, Estonia, Dvina River and Kanin stopover sites identified in Fig. 5.3 are marked (from Eichhorn 2005).

individuals indicated that one-fifth of the Spitsbergen population made at least a short stop at this pre-breeding station where they gained considerable fat stores (Hübner 2006). Individual fat stores at the Norwegian staging site, as revealed by the abdominal profile index (for calibration of this technique see Madsen and Klaassen 2006), were a good predictor of breeding success in that season (Prop et al. 2003).

Although lay dates were not obtained for the Light-bellied Brent *Branta bernicla hrota* studied during spring migration by satellite telemetry (Clausen et al. 2003) these data again point to a role for 'import' of nutrients for breeding. One pair (each carrying a transmitter) migrated from Denmark (departure 30 May) to NE Greenland (arrival 2 June, final destination 4 June) and subsequently returned with at least one gosling. Stopover during this epic spring journey (c. 3500 km) was extremely limited (48–59 hours) and Clausen et al. (2003) presume laying occurred within one week of arrival. These findings point to a role for endogenous fat stores to support breeding, in keeping with data on carcass analysis of geese of the same species studied at a breeding station in Canada (Ankney 1984). Recent tracking studies on Pink-footed Geese *Anser brachyrhynchus* by Glahder et al. (2006) provide a detailed itinerary for individuals followed from Denmark via Arctic Norway to the breeding grounds on Spitsbergen. Although again lacking precise laying dates for the individuals tracked, the timing makes the conclusion inescapable that egg formation is already underway before the geese reach the Spitsbergen archipelago ('eggs made in Norway', Glahder et al. 2006). Intensive observation of marked individuals during staging at a pre-breeding site on Spitsbergen showed an increase in abdominal profile despite the brief stop, indicating 'income feeding' supplementing the capital investment the geese brought from Norway.

Klaassen et al. (2006b) review a long-term data set for the Lesser Snow Goose *Anser c. caerulescens* on the interval between arrival at the La Pérouse colony (Hudson Bay) and laying of the first egg. Analysis of stable isotopes in the egg components compared with local food sources and the maize exploited at stopovers on agricultural land were obtained from another data set and allow a preliminary allocation to 'capital' or 'income' breeding. On this basis income breeding prevailed in 5 seasons (typified by long delays on the breeding grounds before laying), whereas capital breeding was implicated in 11 seasons, with 2 seasons qualifying as border-line cases. Clearly the Lesser Snows are opportunistic in their reliance on 'imported nutrients' and follow a flexible strategy depending on local circumstances. We will consider the degree to which Greater Snow Geese *Anser caerulescens atlanticus* depend on fat from body stores for laying and incubation in the following section.

3. A preliminary fat budget for spring migration and breeding in the Barnacle Goose

Eichhorn and co-workers have studied the dynamics of body stores in Barnacle Geese from birds captured or shot before departure from the Wadden Sea, at staging sites in Arctic Russia, and upon arrival at the nesting colony. We will

present this here in the form of a fat budget, as lipids provide the lion's share of the energy budget (92%) and this can be compared to breeding costs, again in terms of fat. At some sites maximal fattening rates were established following the methods of Prop and Deerenberg (1991). Reconstruction of body mass changes during migration hinges on converting flight hours (from the satellite transmitters) to the energetic equivalent of one hour of flight = expenditure of 7 g fat from the empirical physiological studies of flight in this species undertaken by Butler and his team (Butler et al. 1998; 2000; 2003). The predicted changes in the fat stores in the female Barnacle Goose are displayed in Fig. 5.5, together with a provisional budget for breeding. During incubation it was possible to weigh birds on the nest, and obtain estimates of the fat stores in the body from isotope dilution studies and hence derive a measure of fat utilisation (ch. 7). It will be noted that at hatch only a modest residue of fat is still in the body. Incubation requires a contribution far in excess of that needed to form the eggs and develop the oviduct. Requirements for clutch were estimated as in Drent et al. (2003) and oviduct costs from Vézina and Williams (2003; 2005). The fat stores originally laid down in the Wadden Sea suffice to pay for the 2225 km migration to the first major stopover sites in the White Sea (Dvina region) and still leave a sizeable margin. By the time the birds reach the breeding colony further flight costs have been incurred for the additional 1000 km (here booked as one flight for simplification) but additional fat stores have also been laid down. Quantitatively the original fat stores from the Wadden Sea may represent as much as 40% of the stores available to the breeding female when she starts her clutch. Geese observed directly after completion of a major flight generally drink and sleep for extended periods before resuming feeding (as noted for other migrants, see Schwilch et al. 2002) and this 'lost time' is included in the first two days of the journey. Another loss of feeding time occurs just before commencing the clutch. Individuals we watched the last day before the first egg is laid spent much of the time resting rather than feeding, hence the interruption in accumulation of fat stores at that time in the figure.

Intensive observations of individual Greater Snow Geese supplemented by sampling of body stores from birds collected both in the colony and along the flyway (Gauthier et al. 1992; Choiniere and Gauthier 1995; Bêty et al. 2003; Gauthier et al. 2003; Bêty et al. 2004) provide a reliable budget for comparison. Almost half (44%) of the fat supplies accumulated by females during spring staging on the St Lawrence are depleted during the 3000 km migration to the breeding area, Bylot Island (this compares to the decrement of 44% between Wadden Sea and White Sea in the Barnacle Goose). Judging from isotope signatures of body tissues of birds departing from the St. Lawrence and arriving at Bylot, accumulation of additional body stores en route between these points is negligible. With respect to egg production, Greater Snows follow a mixed capital/income strategy where nutrients are obtained from food ingested on the breeding grounds as well as from the body stores. There is evidence that females draw on body fat to pay part of the metabolic cost of incubation, confirming the older findings of Ankney (in Afton and Paulus 1992). Reproductive success peaks within a narrow time window, and

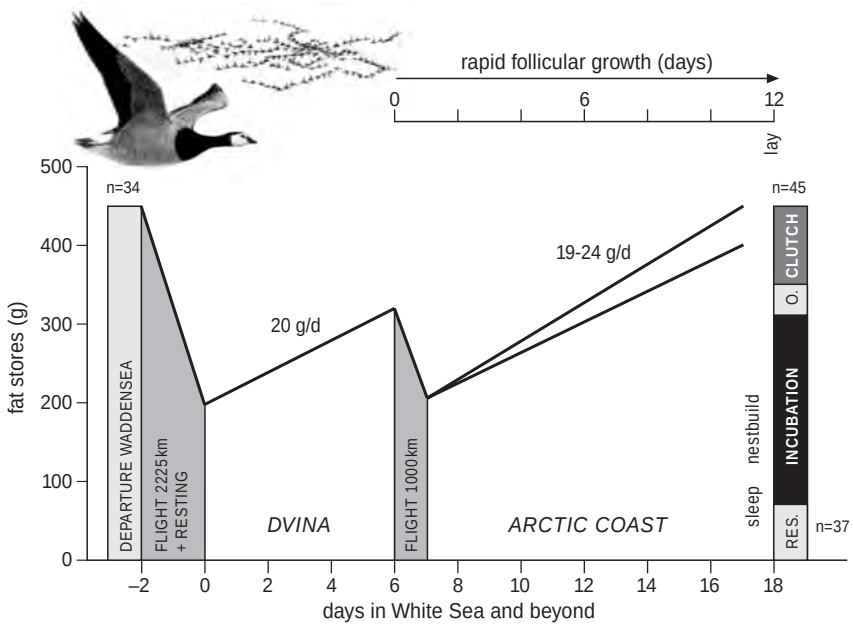

Figure 5.5. Preliminary fat budget for spring migration and successful breeding in the Barnacle Goose following the flyway depicted in Fig. 5.3, and the timetable derived from ten satellite-tagged individuals in 2005. The fat stores at departure from the Wadden Sea (n=34) and arrival at the nesting colony (n=45) are derived from samples of captured and shot birds, respectively, and the dynamics of fat stores at the Dvina stopover are extrapolated values (see text). The fat budget for breeding allows for a modest residue at hatch (n=37 females sampled during incubation). A timetable for rapid follicular growth is shown above. Note that the mean date of arrival in the colony is 4–6 days before lay.

contrary to expectation the earliest birds are not at an advantage. A relatively early arrival implies bridging a long gap before laying, with depletion of body stores not matched by local intake. The most successful individuals arrived about 3 days before the median, avoiding the poor prospects of both early and late birds.

4. Matching spring movements with plant growth: the Green Wave

The green wave hypothesis (Drent et al. 1978; Owen 1980) predicts that avian herbivores time their spring migration along the climatic gradient from temperate staging sites to their Arctic breeding grounds to match the spring flush of plant growth as it sprouts along their route. The geese thus surf along a wave of forage availability, 'riding the crest of the green wave' along their traditional flyway. Van der Graaf et al. (2006b) have examined the match between vegetation and geese by meticulous study of forage growth at two staging sites and the final destination on the breeding station of a specific population of the Russian stock of the Barnacle Goose. Nutritive quality was measured as N content (as a proxy for protein content) of plant species exploited by the geese and expressed as g N per square

meter to include biomass (measured by clipping of aboveground material). At all three sites this measure of potential forage shows a domed shape in relation to date (quadratic function) with the local peak displaced by approximately 100 days along the flyway from the Wadden Sea to the Arctic coast in Russia 3500 km away. Geese departed from the Wadden Sea when the local forage was past its peak, and this pattern held for the Baltic staging site (Gotland) as well, strongly reminiscent of the findings of Prop et al. (2003) for the same species followed along the flyway from Scotland to Spitsbergen. Prop et al. (2003) documented migratory movements in relation to the timing of peaks in local food quality, and their results argue for an eviction of the birds as quality declines. The next stepping stone thus provides respite, because of the relative delay in spring growth. Van Eerden et al. (2005) collated migratory passage dates for Barnacle Geese of the Russian population with dates of commencement of local grasses and sedges as deduced from the relationship with cumulative temperature thresholds established from agricultural research. Long-term temperature records from strategic weather stations along the route were employed for this calculation (five steps). Goose movements tracked vegetation development throughout the flyway, but as in the direct measurements on plant quality and biomass undertaken by Van der Graaf et al. (2006b) arrival on the breeding grounds was 'ahead of schedule'. Presumably arrival in the Arctic (with egg laying commencing shortly thereafter) is timed to enable the newly-hatched goslings to profit from the local food peak. Van der Jeugd et al. (subm.) have indeed shown that laying dates in the colony in question match the survival prospects of the offspring (parents lay at the optimal time, neither too early or too late, with sharp cut-offs at each extreme). To recapitulate, the progression of geese along their spring flyway matches the timing of the nutritious early growth of their major food plants, but arrival on the breeding grounds is timed well in advance of the local peak supply in order to ensure survival of the offspring when they hatch (see Fig. 5.6).

McNaughton (1979; 1984) postulated an intimate mutual relationship between herbivores and their food supply, and suggested that migratory populations via their intensive grazing might elicit a short-term positive response by the target plants. This stimulation of above-ground growth would provide a bonus for the herbivores ('grazing optimisation') particularly welcome because the ratio between fresh shots and old growth would be enhanced. Not only might this influence the duration of exploitation of the new growth by the original consumer, but perhaps also facilitate utilisation by other species following in their footsteps. This issue has also been investigated in the Barnacle Goose (Van der Graaf et al. 2005; Stahl et al. 2006). Detailed measurements were undertaken on the vegetation (*Festuca rubra* swards on the salt marsh) in conjunction with a regime of experimental grazing by captive geese in early spring designed to mimic the natural grazing pressure. Grazing significantly affected sward characteristics, reducing the proportion of dead biomass, and indeed culminated in an increase in potential harvest (in yield of N per square meter) for grazed as contrasted to ungrazed swards. At grazing pressures simulating the cumulative usage by wild geese (15 grazing minutes per square meter) these facilitative effects increase the carrying capacity of the site (yield to grazers) by

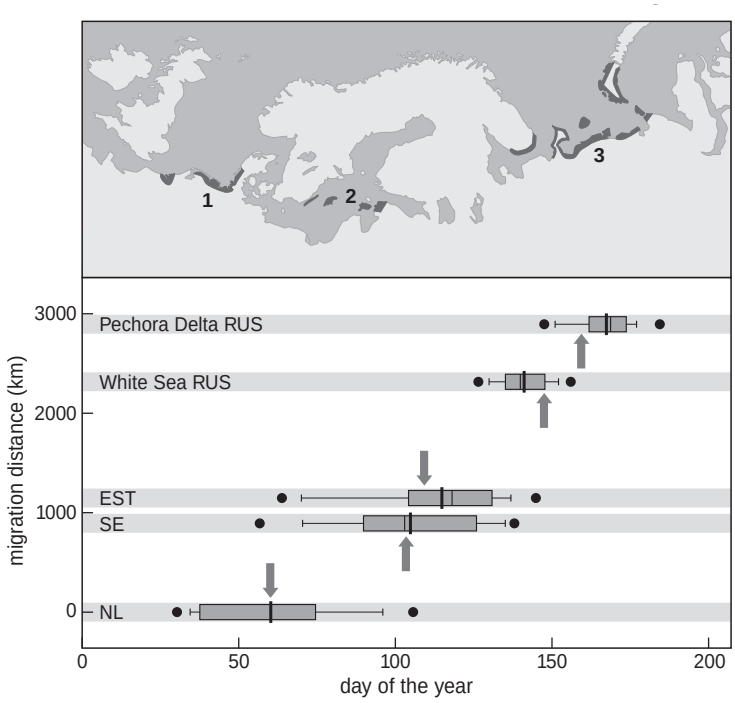

Figure 5.6. Migratory timing of the Russian population of the Barnacle Goose (heavy arrows) in relation to commencement of spring growth of grasses along the flyway (box diagrams enclose central 75%, the dots delimit 5% and 95% of predictions from 20 years data set, median = thin crossbar, mean = heavy crossbar). Adapted from Van Eerden et al. 2005; observation sites indicated in map, 1 = Netherlands NL, 2 = Sweden SE and Estonia EST, 3 = Pechora delta.

about 20% compared to lower intensities. Increasing grazing pressures above the values that match usage by the wild flocks however did not lead to further increments: the unrestrained birds had already achieved an optimal grazing pressure. These advantages can only be reaped in areas free of human disturbance, where the geese can impose their grazing pressure without restraint (Bos and Stahl 2003). Taking the second facet of McNaughton's idea, there is some evidence that the wild herbivores at this spring staging site can profit from each other as the waves of two migrant goose species interact with the resident hares (Stahl et al. 2006). So far there is no evidence for a growth-stimulation due to grazing in temperate salt marshes, but overwhelming evidence that grazing by geese enhances the *quality* of the food on offer. In the sub-Arctic salt marshes of the Hudson Bay lowlands Hik and Jefferies (1990) demonstrated that intensive goose grazing (by Lesser Snow Geese) enhanced productivity of their target food plants *Puccinellia phryganodes* and *Carex subspathacea*. In this nitrogen-limited system the increase of above-ground biomass depended entirely on nutrient inputs leaching from the goose droppings (acceleration of N cycle).

Discussion

Our conclusion that Arctic waterfowl (at least above a lean body mass of 1 kg) must of necessity supplement local foraging by drawing on body stores for egg formation and incubation is in agreement with the analysis of Nolet (2006). Nolet modelled the dependence on body stores for breeding in relation to the energetics of migratory travel, under the constraint of reaching the goal in time to lay eggs at realistic dates. He found that all six species of Arctic waterfowl where speed of migratory travel had been measured empirically by tracking (ranging from Pintail *Anas acuta* on through Arctic-nesting swans) must depend to some degree on body stores for successful reproduction. Recently, a massive tracking exercise on Pintail (n=130) revealed that individuals breeding in subarctic Alaska on the tundra of the Yukon Delta originated from wintering quarters of the central valley of California. Virtually all intercalated a 2-month spring staging period in the Oregon-California border region, and the early nesters took a 'direct' route onwards to the Yukon (3250 km) without extensive stop-over (Miller et al. 2005). Esler and Grand (1994) had previously shown that Pintails nesting in this region showed a heavy reliance on lipid stores in the body early in the season (large 'endogenous reserves' being needed for the clutch as well as for maintenance). Mann and Sedinger (1993) in another Alaskan study confirmed that lipid stores were drawn upon for both egg formation and maintenance. The tracking data make it likely that these critical fat stores are in fact 'flown in' from the spring feeding sites more than 3000 km away.

Newton (2006) and Drent et al. (2006) have collated the evidence collected to date on the positive association of body weight at migration time and subsequent breeding success (mainly in waterfowl). It is our thesis that the causal link behind this association is the absolute necessity to arrive on the breeding grounds with adequate body stores. Arzel et al. (2006) have provided a massive compilation and point out that information on ducks (19 species tabulated) is often inadequate to decide whether endogenous or exogenous sources are relied on, in contrast to the dominant pattern of an endogenous contribution in geese and swans. In contrast to geese, ducks are more amenable to long-term feeding experiments in captivity and the results reported by Barboza and Jorde (2002) for *Anas rubripes* would repay following up to quantify the endogenous component in egg production and incubation. Gunnarsson et al. (2006) provide evidence on the migratory timing of individual Black-tailed Godwits (*Limosa limosa lapponica*) wintering in Europe and breeding in Iceland that links the quality of the wintering site (judged by prey intake rates and survival) with the quality of the breeding stations (traditional sites conferring enhanced success). Marked individuals utilizing the 'high quality' wintering sites (presumably achieving superior body condition) arrive earlier in Iceland and settle in the best breeding habitat. Such complex 'carry-over' effects from wintering or staging sites to the breeding area will doubtless prove the rule, with competition sorting the individuals at each stage.

These findings do not imply that all birds nesting in Arctic regions carry sufficient body stores with them to form the eggs. Especially for passerine migrants

breeding at high latitudes, the role of endogenous reserves brought into the breeding grounds is still debated, and evidence based on individual migration itineraries is extremely difficult to obtain and therefore very scarce (Benson and Winker 2005, Smith and Moore 2003). However, given the stringent nesting schedules in arctic environments we would be greatly surprised if any waterfowl or shorebird species can complete *incubation* without drawing on body stores. Results from analysis of stable isotopes argue against a role of endogenous nutrients in egg formation of several shorebird species in the Arctic (Klaassen et al. 2001). Given the staggering costs of incubation in this group (Piersma et al. 2003) a subsidy from body stores is inescapable during this phase (note that females are the sole incubators in many shorebirds). Direct assessment of the provenance of body stores (especially fat) in incubating shorebirds by means of stable isotopes is an exciting avenue to follow up. We would argue that shorebirds may not be 'capital layers' but (when including egg care) must be considered 'capital breeders'. Morrison (2006) adduces indirect evidence for the Red Knot *Calidris canutus* in support of this contention. The validity of the premise that management of the state of body stores is a closely-run affair for the incubating female can be demonstrated directly for waterfowl. In a three-season study on the Wood Duck *Aix sponsa* Hepp et al. (1990) found that in the year of steepest mass loss during incubation, females heavy at hatch returned at higher rates to nest the next year than females light at that time. In the Common Eider, a species that as noted does not feed at all during incubation, Hanssen et al. (2004) and Hanssen (2006) working in Arctic Norway have revealed the narrow margins that apply to mass loss if the female is to complete brood care and return to breed the next season. By experimentally inducing an immune challenge (injection of non-pathogenic antigen, i.e. sheep red blood cells) in incubating hens 5 days after completing their clutch, daily mass loss increased compared to a control group (injected with sterile saline). Over an eight-day interval the 'challenged' birds had lost 225 g body mass (initial mass 1910 g) compared to a 195 g loss in the controls (initially 1980 g) and time to hatch was 0.6 days longer. Remarkably, in the 'challenged' birds the tendency to tend the brood that year was *increased*, but their return rate the next season was only half that of the controls. Admittedly, this is a complex experiment, but it can be argued that from the viewpoint of body condition even a modest degradation (heightened mass loss) during incubation equates with far-reaching fitness repercussions. Apparently, during their long fast incubating waterfowl are highly susceptible to upsets in the immune system (Hanssen et al. 2004).

If as we argue waterfowl and shorebirds follow the strategy to arrive in the breeding areas with body stores critical to see them through incubation, this will influence their migratory policy. Alerstam (2006b) expands on this consideration and emphasises that the crucial issue is the ability to exploit final stop-over sites providing deposition rates of body stores in excess of what can be attained at the breeding destination. For the calculation the gain at the stop-over must be discounted for the costs of the flight still to be undertaken (see also Nolet and Klaassen 2005).

The tracking results for Arctic geese reviewed here support the contention that egg formation commences well before the birds reach the nesting colonies. In cases where the female has already entered the Arctic regions we are faced with the need to define 'endogenous' and 'exogenous' sources more precisely. For simplicity we here advocate reckoning the immediate vicinity of the nesting site (localities that can be reached in minutes rather than hours of flight) as belonging to the 'breeding grounds'. In contrast, directed flight from stop-over sites at distances of 50 kilometres or more would qualify as part of the migratory journey, and nutrients garnered at that distance would strictly speaking be 'endogenous'.

According to the 'Green Wave hypothesis' spring movements track the onset of spring growth along the flyway. Our examination of this concept provides support for the notion along the route, and points to a narrow window of opportunity at each site. Late birds face depleted resources (Nolet and Drent 1998) and a decline in nutritive quality (Prop et al. 2003; Prop 2004) and will be penalized. The geese arrive on the breeding grounds well in advance of the local growth spurt, and it appears that egg laying is timed to ensure that the goslings can exploit this resource. In this view, the use of body stores by the adults early in the season, before they can satisfy their requirements locally, is an adaptation to allow matching hatch dates to the optimal seasonal window. Similarly, the fattening rates of Pink-footed Geese (inferred from changes in the abdominal profile of marked individuals) are much lower upon arrival on the breeding grounds (Spitsbergen) than at stop-over sites along the Norwegian coast exploited after departure from Denmark in early April (Klaassen et al. 2006a). Klaassen and co-workers (Tombre et al. 2005; Klaassen et al. 2006a) have modelled progression of the Pinkfeet along the spring flyway using dynamic programming and taking account of how intake rates are impacted by human disturbance at the stopover sites. In general terms the geese adhered to the predictions of the Green Wave, but the scaring campaigns resulted in redistribution of the Pinkfeet along the flyway, and impinged negatively on breeding success. Similarly, human disturbance at the spring staging sites of the Greater Snow Geese along the St. Lawrence estuary in Canada has deleterious effects on breeding at their high Arctic nesting grounds 3000 km away (Béchet et al. 2004).

Although geese with the advantage of their cultural traditions in migratory habits provide numerous examples of flexibility in response to environmental change in the past (Sutherland 1998) the question arises whether they will be able to cope with the increased tempo of change expected in the near future (Stervander et al. 2005). Climate change models (IPCC 2001) call attention to the discontinuities in regions spanned by avian migrants in their annual cycle. There is already compelling evidence that conflicting trends affecting climate in winter, the spring stopovers and the breeding grounds in the insectivorous Pied Flycatcher *Ficedula hypoleuca* have disrupted the match between food supply and spring arrival (Both et al. 2006). Breeding is no longer within the optimal time span in favoured habitats in temperate Europe and there is evidence for population declines resulting from a fall in reproductive output. Møller, Fiedler and Berthold (2004) have recently reviewed the topic of 'Birds and climate change' and we will merely touch here on

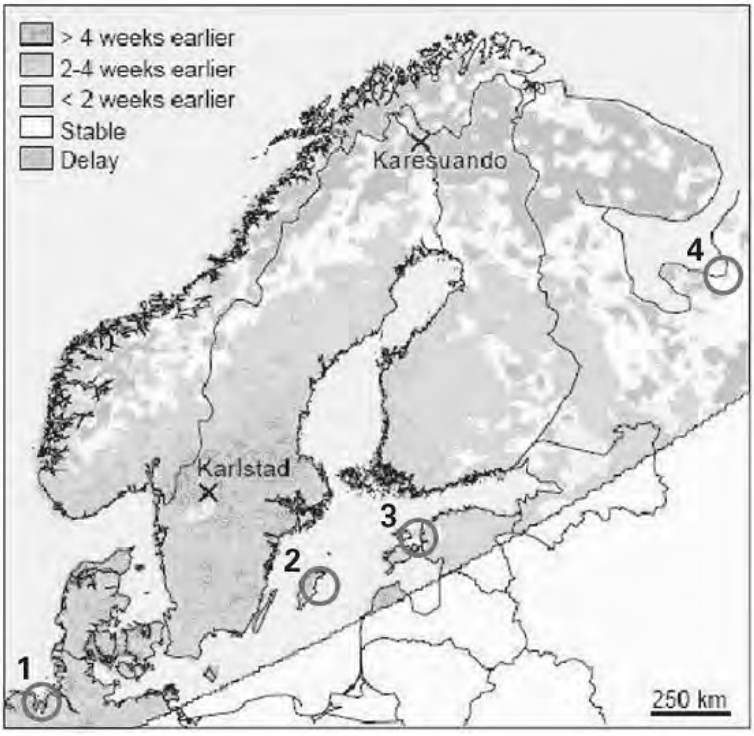

Figure 5.7. Change in onset of spring (see colour key) 1981-1998 along the migratory route of the Barnacle Goose en route from the Wadden Sea (1) via Gotland, Sweden (2) and coastal Estonia (3) to the Dvina delta (4) in the White Sea, a vital stopover before reaching the breeding colonies on the Arctic coast (not shown). Onset of spring plant growth for the 17 year period was derived from NDVI values (resolution 8 km). Modified from Høgda et al. (2001).

events that potentially can disrupt the NE Atlantic flyway. We have shown that the Russian population of the Barnacle Goose proceeds along the climatic gradient in spring, timing its stopovers strategically to coincide with the local flush in nutritious spring growth. By employing cloche-type miniature greenhouses in the Wadden Sea, Baltic and at the breeding colony on the Barents Sea, Van der Graaf and co-workers (Van der Graaf 2006) simulated the effects of an elevation of 1° C on spring growth in the forage plants the geese depend on. These data provide inputs to model the impact of climate change on the timing of spring growth, and point to a weaker response in the Arctic. A temperature rise of 1° (prediction of the IPCC 2001 for the period until 2050) would advance plant growth in the Wadden Sea and Baltic by eight days, but at the Russian breeding site by only four days due to the strong impact of freezing temperatures well into May. This discrepancy is aggravated by the uncoupling of climate change documented by the regional model of Høgda et al. (2001) with continuing warming of the Baltic region but no change

or even regression in the Arctic regions adjacent to our study area (see Fig. 5.7). Indeed, weather records collected at Naryan Mar (close to our goose colony) over the past 35 years fail to reveal a warming trend, in contrast to increases at stations in the Baltic and Wadden Sea (Van der Graaf 2006). If the geese respond to the earlier 'spring bite' along the flyway they would thus arrive on the breeding grounds with a lengthened delay until local plant growth starts. The ability of the Barnacle Goose to cope with these desynchronised patterns of spring growth will thus depend heavily on exploiting staging opportunities in the White Sea, especially coastal wetlands where local animal husbandry has traditionally maintained swards attractive to geese. A complicating factor is the decline in this small-scale animal husbandry in the region, reducing the extent of hayfields and riverine meadows managed for cattle. Parallel changes have been documented in coastal communities in Estonia in recent decades (E. Puurmann in Hallanaro and Pylvänäinen 2002) leading to a loss of goose habitat for spring feeding (A. Leito pers. comm.). These complexities warn against assuming that these migrant birds will always be able to cope successfully with a mismatch in rates of environmental change at various points of their annual trajectory.

Climate change goes hand in hand with change in land use as agricultural developments ebb and flow, and virtually all goose populations now face a "squeeze" where the patches of natural habitat providing forage become increasingly restricted. The ability to shift to habitats dominated by agricultural crops differs between the species and season, and recent reviews stress the uncertainties associated with ongoing change (Abraham et al. 2005; Gauthier et al. 2005; Ward et al. 2005; Fox et al. 2005; Van Eerden et al. 2005); Jefferies et al. (2006) point out that current agricultural policy in both North America and Europe will tend to reduce the acreage and quality of crop foods available to geese in winter (and in many populations spring as well, see e.g. Percival and Percival 1997). Taking a broader view to include all waterfowl, Long et al. (2007) point out that in Central and South America, Africa and Asia in fact the majority of populations are now in decline, driven by loss of wetland habitat (climate and man conspiring) and a variety of anthropogenic factors. The complacency we might feel from the perspective of Europe and North America where decreases are in the minority is thus misplaced.

Acknowledgements

We thank the contributors to the 2004 Workshop *Travelling to Breed* of the European Science Foundation for sharing their findings with us (available in ARDEA 94(3), 2006). Our fieldwork was supported by the European Science Foundation (BIRD Programme Optimal Migration in Birds), the Netherlands Organisation for Scientific Research (Netherlands Arctic Programme), the Schure-Beijerinck-Popping Fonds of the Royal Netherlands Academy of Sciences, and Groningen University. GE was financially supported by scholarships from the 'Marianne und Dr. Fritz Walter-Fischer Stiftung', Germany, and the 'Ubbo Emmius Programme' at the University of Groningen. JS acknowledges financial support from the 'Deutsche Forschungsgemeinschaft'.

Part

III

Why travel to breed: arctic and temperate breeding compared

Chapter

6

Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply

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Global Change Biology (in revision)

Abstract

Within three decades, the barnacle goose population wintering on the European mainland has undergone a dramatic change in breeding range and numbers not only in its arctic strongholds but through colonisation of new breeding areas to the southwest. Such rapid range expansions provide information on how species adapt to novel environments, and are highly relevant to the study of global change. Three recently established populations, one arctic (Barents Sea) and two temperate (Baltic, North Sea), have been subject to long-term studies. The Baltic population has a considerably shorter migration route compared to the Arctic one, whereas birds from the North Sea populations are non-migratory. Birds in the Baltic and North Sea populations breed six to seven weeks earlier than birds from the Barents Sea population. Timing of wing moult in the temperate populations only advanced by two to four weeks. In the Barents Sea population, there is strong stabilizing selection on timing of breeding, and the timing of egg-laying appears optimal with respect to the peak in food availability. In the temperate populations timing of egg-laying is too late in relation to the peak in food availability, and there is moderate to strong directional selection for early breeding. In the Baltic population, absolute timing of egg-laying has advanced considerably in keeping with global warming over the twenty-year study period, but advanced little relative to spring phenology, and selection on laydate actually increased. Without analysing extensive data on how individuals have responded over the years we cannot evaluate the interaction between evolutionarily driven genetic change, phenotypic plasticity and age-effects on timing of breeding.

Because timing of breeding advanced more than timing of wing moult, synchronisation between wing moult of parents and fledging of young has disappeared in temperate populations. The recently established southern populations of barnacle geese are currently not completely adapted to their environment. Nevertheless, they were initially able to grow at an astonishing rate. These rapid changes probably result from a combination of reduced human prosecution and changes in land use. Increasing density-dependent effects in the original arctic breeding area may also have contributed to individuals starting off seeking greener pastures elsewhere in the species range.

Introduction

Understanding the mechanisms by which species adapt to shifting climatic zones is crucial to predict the impact of global change. Recent studies mainly emphasised the *inability* of species to adapt sufficiently to rapidly changing environments (Verhulst et al. 1995; Both and Visser 2001; Visser and Holleman 2001). Especially long-distance migrant birds seem vulnerable to large scale climatic change, because they rely on a whole series of environments at different times during their annual cycle, and these may change at different rates (Both et al. 2006; Sanderson et al. 2006; Jonzén et al. 2006). However, studies of migratory species that, *in contrast*, have been very successful in spreading into new environments are equally relevant to the study of global change, because such studies provide information on how well species can adapt to different environments, and thus provide information about the limits of their plasticity. Rapid range expansions along a north-south gradient are particularly useful, as these give information on adaptation to different climatic zones, and can therefore serve as natural experiments in which large shifts in climate can be studied in a relatively short time span.

Species ranges have contracted and expanded many times during evolutionary time as a response to shifting environmental conditions. Some species, for example the finches of the genus *Carpodacus* seem more prone to rapid range alterations than other species, most probably as a result of their remarkable capability of rapidly evolving new adaptations to novel environments (Badyaev and Martin 2000; Badyaev et al. 2002). Many historic range alterations also involved major changes in migratory behaviour. In some cases, for example that of the blackcap *Sylvia atricapilla*, the change in migratory behaviour resulted from selection on genetically determined variation (Berthold et al. 1992; Pulido et al. 2001). Indeed, most passerines seem to have genetically determined migratory behaviour (Van Noordwijk et al. 2006). However, in a review of recently documented rapid shifts in migratory behaviour, most cases were confined to species with extended parental care, such as waterfowl, where information on timing and direction of migration is transmitted culturally (Sutherland 1998). Although changes in breeding range or migratory behaviour have frequently been described, studies in which the performance of individuals in historical versus newly colonised environments, or of individuals adopting traditional versus novel migration strategies are rare (Eichhorn et al. 2006).

Here we compare three populations of the barnacle goose *Branta leucopsis*, one arctic (Barents Sea) and two temperate (Baltic, North Sea), that have all been subject to long-term studies. The species has long been considered a specialist of the high Arctic, benefiting from the short but productive arctic summer at the cost of a long migration route and severe environmental conditions. However, it now seems to be rapidly adapting to a wide range of habitats in the temperate zone, thereby considerably shortening the migration route, or even giving up migration altogether. Human impacts must also be included as causes of these range changes (Van der Graaf et al. 2006a). These rapid changes raise questions about the limits of plasticity and the possibility of rapid evolutionary change. We compare major life-

history characteristics between these populations, focussing on timing of reproduction in relation to food availability. We will show that, despite their initial rapid increase and general success, temperate populations of the barnacle goose are currently not completely adapted to their novel environment, mainly due to a constraint on early breeding.

Material and methods

Study populations

In recent decades, the East Atlantic Flyway population of barnacle geese *Branta leucopsis* has undergone a dramatic change in numbers (Ganter et al. 1999). In the 1960's the population numbered ca. 25 000 individuals. By 2006, it had increased more then twenty-fold to an estimated 550 000 individuals (SOVON unpublished). This increase went hand in hand with the colonisation of new breeding areas to the west and southwest of the original breeding grounds on Novaya Zemlya and Vaigach in arctic Russia, including our recently established study colony in the Barents Sea.

In 1971, the first breeding pair in the Baltic was found (Larsson et al. 1988), and since then this population has grown at a spectacular rate, numbering 17 000 individuals in 1997 (Larsson and Van der Jeugd 1998) and approximately 21 000 individuals in 2005 (Larsson unpublished). During the 1980's, barnacle geese also expanded westward along the Barents Sea Coast (Filchagov and Leonovich 1992; Syroechkovsky Jr. 1995). Present numbers along the Western Barents Sea coast, including the island Kolguev, are not well known, but are likely to exceed 60 000 breeding pairs (Anisimov et al. unpubl.). More recently, a population was established in the southwest of the Netherlands (Meininger and Van Swelm 1994; Ouweneel 2001). Here, the first breeding pair was encountered in 1981, and since then, the North Sea population has been growing rapidly and numbered 25 000 individuals in 2005 (Van der Graaf et al. 2006a; Voslamber et al. 2007). During the same period, barnacle geese have also appeared as breeding birds in other western European countries. All recently established breeding areas are situated within the flyway, i.e. they are confined to historical wintering areas and staging grounds of the species.

Thus, within the East Atlantic Flyway, three breeding populations of barnacle geese, the Barents Sea, Baltic and North Sea populations, are now recognised (Fig. 6.1), of which the Barents Sea population greatly outnumbers the other two populations. Birds from these populations share the same wintering grounds, but habitat choice on a smaller scale differs (Van der Jeugd et al. 2001). Observations of colour-ringed birds with known origin indicate that there exists some exchange of, predominantly male, individuals between populations, and a limited amount of gene-flow between the different populations along the east-Atlantic Flyway is therefore likely to occur (Van der Jeugd and Litvin 2006).

Long-term studies have been initiated within each of the three populations (Fig. 6.1). In the Baltic, birds breeding in the oldest and largest breeding colony situated at Laus holmar (57°17'N; 18°45'E) off the east coast of the island of Gotland,

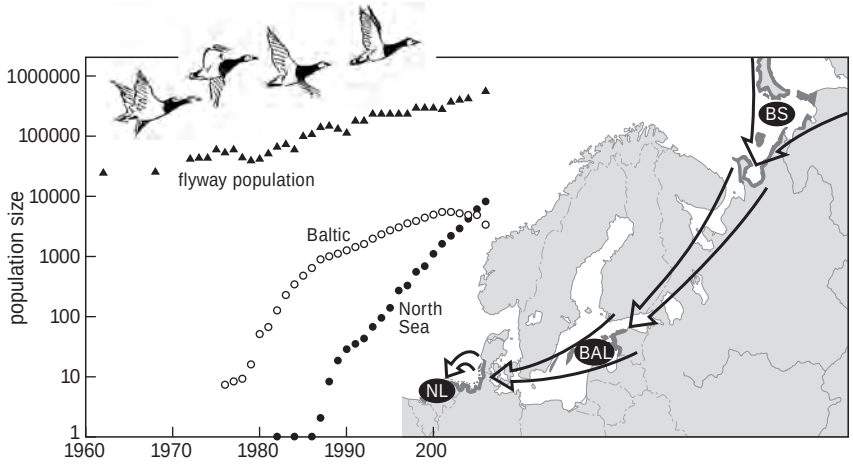

Figure 6.1. Number of breeding pairs for two recently established temperate barnacle goose populations (Baltic and North Sea, open and closed circles), and the total number of barnacle geese of the east Atlantic Flyway (closed squares). Letters in the map indicate the position of the study sites: BS (Barents Sea), BAL (Baltic), and NL (North Sea). Arrows indicate the migration route Arctic and Baltic birds follow to their wintering grounds. Birds from the North Sea population are sedentary.

Sweden have been studied from 1984 to 2006 (Larsson et al. 1988; Larsson and Forslund 1994; Larsson et al. 1998). During the 20-year study period, this colony increased from 450 to a maximum of 2 450 breeding pairs. During recent years, the number of breeding pairs has declined due to predation and disturbance by red foxes and white-tailed eagles. A more detailed description of the study area can be found in Larsson et al. (1988) and Van der Graaf et al. (2006a; 2007a; 2007b). In the Barents Sea population, a colony on the northwest coast of Kolokolkova Bay, near the abandoned settlement of Tobseda, Malozemelskaya Tundra, northern Russia (68°35'N, 52°20'E), has been studied annually between 2002 and 2006 (Van der Jeugd et al. 2003; Van der Graaf et al. 2004; Eichhorn et al. 2006). The colony comprised between 1 200 and 2 000 breeding pairs during our study. Barnacle geese have bred in the study area since at least 1994 (Syroechkovsky Jr. 1995). In the North Sea population, barnacle geese were studied between 2004 and 2006 at Hellegatsplaten (51°42'N, 4°20'E), one of the largest colonies in the Delta area in the southwest Netherlands. This colony consists of several breeding sites, mostly situated on islands that resulted from the reclamation works undertaken in the Volkerak reach of the Rijn / Maas delta. The total number of nests varied between 518 and 537 during the three study years (Pouw et al. 2005; Van der Jeugd et al. 2006).

Capturing, marking and measurement techniques

In each of the three study populations, moulting flocks of breeding and non-breeding adult and juvenile barnacle geese were captured annually at moulting localities in July (Baltic and North Sea) and August (Barents Sea) using a rounding-

up technique (Ogilvie 1978). In addition to moult catches, a small number of females were captured with clap nets during incubation. Captured birds were ringed with engraved coloured plastic leg rings and with metal rings. Approximately 5 500 individual birds were colour ringed in the Baltic between 1984 and 2000 (after 2000, no new colour rings were applied during moult catches), 1 400 in the Barents Sea between 2002 and 2005, and 420 in the North Sea population in 2004 and 2005 (no new colour rings applied in 2006). Sex was determined by cloacal inspection (Owen 1980). Captured birds were aged as juveniles or adults that were one or more years old. Juvenile birds were measured (see below) and weighed upon ringing when they were between three and eight weeks old.

The ninth primary feather, counted descendently, of moulting adult birds and wing length of juvenile and adult birds were measured following Larsson (1996) and Van der Jeugd et al. (2003). In the Barents Sea and Baltic populations, ninth primary feathers of moulting adult birds that were captured twice within the same year grew on average 6.98 mm/day in females (se = 0.13, n = 163; males) and 7.44 mm/day in males (se = 0.15, n = 124). There was no difference in growth rate between the populations ($F_{1,184} = 0.01$, $P = 0.97$), but females tended to grow their primaries slightly slower than males ($F_{1,184} = 3.09$, $P < 0.1$). We calculated the start and end dates of the adult wing moult in all three populations by using the length of the ninth primary upon capture and the sex-specific growing rates reported above (see also Larsson (1996)). Fledging dates of juveniles were calculated using linear regressions of wing length on age (date of capture minus hatch date). Female juveniles grew their wings slower than males, and growth rate of juvenile wings decreased significantly from north to south (Table 6.1). We assumed that birds were capable of flying when they had reached their full-grown wing length (adult males: 420 mm; adult females: 395 mm: juvenile males: 405 mm; juvenile females: 380 mm; own observations).

Reproductive success in relation to lay date

Hatch dates of broods of marked pairs were determined either by direct observations of pairs with young leaving their nests, or by estimating the age of newly hatched young on nearby grazing grounds and then backdating (Larsson and Forslund 1991). In addition, many chicks were webtagged upon hatching in the North Sea and Barents Sea populations. When later caught as fledglings during round-ups, hatch dates of these individuals were known. Fledglings without webtags that were colour-marked during round-ups and seen in the company of marked parents during observations made after capture were assigned the hatch date of their parents nest. Lay date was not routinely recorded in the Baltic, but a number of nests was visited repeatedly in 2003 and 2004. In the Barents Sea and North Sea populations we actively searched for new nests once every two or three days. In all populations, lay date was defined as the day at which the first egg was laid. For incomplete clutches found during egg-laying, lay date was estimated as follows: 1 egg: day of discovery; 2 eggs: day of discovery minus 1; 3 eggs: day of discovery minus 3, 4 eggs: day of discovery minus 4; 5 eggs: day of discovery minus

Table 6.1. Growth rate of juvenile wings based on regression of wing length on age (age x sex: $F_{1,1020} = 3.76$, $P = 0.05$; age x population: $F_{2,1020} = 63.64$, $P < 0.0001$). Letters denote which populations differ significantly from each other.

	Females			Males		
	mm / day	se	n	mm / day	se	n
Barents Sea [a]	8.74	0.64	88	10.03	0.91	87
Baltic [b]	8.63	0.40	425	9.10	0.38	405
North Sea [b]	7.25	1.56	9	9.55	0.93	14

6). This method differs slightly from the one used by Lepage et al. (1999) in that we subtracted one day more for clutches of 3 and 5 eggs.

The median interval between lay – and hatch date for nests where both lay date and hatch date were recorded averaged 30 days without any difference between populations ($F_{1,415} = 0.01$, $P = 0.99$). To be able to express reproductive output as a function of lay date, we calculated lay date as hatch date minus 30 days in all cases where hatch date was known but lay date was not known from direct observations.

Number of fledged young per pair was defined as the number of young in families observed on the day closest to 10 July (within ±14 days) in the North Sea population, on the day closest to 20 July (within ±14 days) in the Baltic population, and on the day closest to 14 August (within ±4 days) in the Barents Sea population. These dates represent the period between one to three weeks before fledging for most individuals. Intraspecific nest parasitism as well as brood mixing after hatching occurred in all populations. In the Baltic, it was found that about 17% of the fledged young are not the true offspring of the adults guarding them (Forslund and Larsson 1995; Larsson et al. 1995). There are currently no data that can confirm these figures for the North Sea and Barents Sea populations. Brood sizes were not adjusted for intraspecific nest parasitism or brood mixing after hatching. Breeding attempts that failed during incubation due to predation or nest abandonment were assigned zero fledged young.

Post-fledging survival in relation to lay date

Post-fledging survival of individual young was estimated using mark-resighting analyses of observations of marked juveniles on the wintering grounds. This is feasible because a network of volunteer ringreaders (nearly 1000 in all) has been built up effectively covering the winter range. In the North Sea and Barents Sea populations, not all juveniles that were caught during round-ups had known hatch dates and/or lay dates. For these young we estimated hatch dates using a regression of age on wing length for each sex separately for juveniles with known hatch dates, and then calculated laydates from these hatch dates as explained above. Regressions explained 88% and 63% of the variation in age in the North Sea and Barents Sea populations, respectively. In total, 36 010 observations of barnacle geese that were

colour-ringed as fledgling in one of the three study populations and that were reported from the wintering grounds by the general public could be used for analyses. 105, 956 and 608 individuals from 2, 13 and 3 cohorts were used in the North Sea, Baltic and Barents Sea populations, respectively. As the number of cohorts differed between populations and partially referred to different years, birds from each population were analysed separately, using Program MARK (White and Burnham 1999). All analyses started from a two age-class model with time-dependence, model ϕ_{a2*t},P_{a2*t} . The first age-class spanned the period between marking and arrival on the wintering grounds in October-November (Van der Jeugd and Larsson 1998) and, hence, measured post-fledging survival. The second age-class spanned all subsequent years and measured adult survival after the first winter. Within both age-classes, survival estimates for different years were identified separately. Model selection was based on a modified Akaike's Information Criterion (AICc, (Anderson et al. 2000). In addition to AIC, we used the ANODEV procedure in MARK to test for the effect of lay date on post-fledging survival. Goodness of fit to the Cormack-Jolly-Seber model was tested using a bootstrap procedure provided in MARK. No adjustments to deviance and AIC were made, as the bootstraps yielded scale parameters ($\hat{c}$) that were less then one for each population, indicating a good fit. After resighting rate had been modelled, a limited number of models for survival were tested to specifically investigate the effect of lay date on post-fledging survival (Lebreton et al. 1992). This was done by first running a model where survival in the first age-class, i.e. post-fledging survival, was held constant among years, and, second, adding individual lay date as a covariate to explain variation in post-fledging survival in this model. The ANODEV test including these two models and the global model (ϕ_{a2*t},P_{a2*t}) specifically tests for the presence of significant effect of lay date on post-fledging survival (Skalski et al. 1993).

We then calculated the number of young that arrived at the wintering grounds by multiplying the number of young observed per nesting female around fledging at the breeding grounds by the predicted post-fledging survival probability that corresponded to the particular lay date of those young. The relationship between lay date and number of fledged young was analysed using separate multiple regressions for each population. Before analyses, lay date was standardized to control for differences in mean lay date among years by first subtracting year- and population-specific means and then adding population-specific means again. We tested for quadratic relationships by including both lay date and lay date^2 as explanatory variables.

Food quality

The quality of forage biomass was determined by taking samples of leaf-tips of the main forage species Red Fescue *Festuca rubra*, Common salt-marsh grass *Puccinellia maritima* and creeping bent grass *Agrostis stolinifera* in the Netherlands and the Baltic region, Creeping salt-marsh grass *Puccinellia phryganodes* and Hoppner's sedge *Carex subspathacea* in the Barents Sea region (Van der Graaf et al. 2006b). Samples were taken at roughly ten-day intervals in 2003 and 2004 throughout the entire breeding season at each site except for the North Sea population, where measures were taken

in 2004 only. At the same time samples were also taken at a major spring staging site in the Netherlands (Schiermonnikoog; Van der Graaf et al. 2006b). Samples were dried at 60°C for 48 hours and analysed for Nitrogen content using an automated CHNS-analyser.

Statistics

All statistics were performed using SAS version 8.2 and SPSS version 12.0.1. All data presented include mean ±SE. The relationships between date and nitrogen content, and standardized lay date and fledgling production were analysed using multiple regressions including linear as well as quadratic terms. Quadratic terms were removed when not significant. Selection differentials were constructed for each population by calculating the difference between the population mean lay date and the mean lay date of all breeding attempts that were successful, weighted for the number of young produced and their post-fledging survival. Selection coefficients were standardized by dividing by the standard deviation of lay date in each population (Falconer 1989).

Results

Timing of reproduction and moult

There were large differences in the timing of reproduction and moult between the populations. On average, eggs hatched on 11 July in the Barents Sea, on 29 May in the Baltic, and on 25 May in the North Sea populations. Thus, whereas there is only a small difference between the two temperate populations, hatching in these populations takes place c. 6 weeks earlier compared to the Barents Sea population (Fig. 6.2). Also the range of lay and hatch dates increased from north to south. In the Barents Sea population, 90% of all nests were initiated within a period of twelve days, compared to 15 days in the Baltic and 36 days in the North Sea population.

Timing of wing moult did not advance as much as hatch date did. In the Barents Sea population, non-breeders started their wing moult on average on 15 July, whereas families leading broods postponed the start of wing moult with c. two weeks to 27 July (Fig. 6.2). The bimodal pattern in the start of wing moult is absent in the Baltic and also in the North Sea population (Fig. 6.2). In these populations, wing moult started around 1 July, only two weeks earlier than in the Barents Sea population.

Hatch date advanced c. four weeks more than timing of wing moult did. Although juvenile birds grew their wings more slowly in temperate populations compared to the Barents Sea population (Table 6.1), this could not fully compensate for the longer time span between hatching and start of wing moult. As a result, synchronisation of wing moult and fledging disappeared in temperate populations, with juveniles fledging on average two weeks earlier relative to the moment their parents regained flight ability compared to juveniles in the Barents Sea population (Table 6.2).

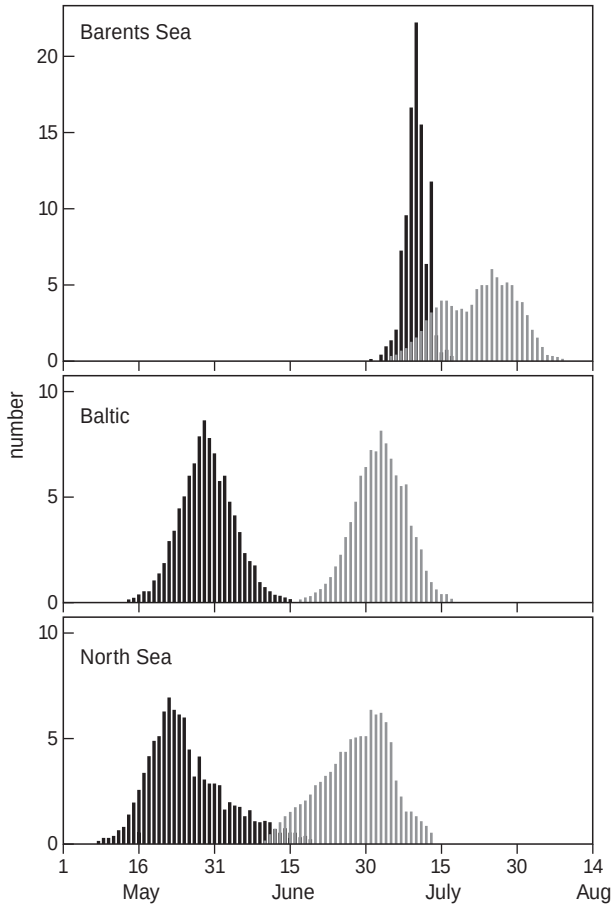

Figure 6.2. Timing of hatching (black bars) and start of wing moult (grey bars). Note the bimodal pattern in the start of wing moult in the Barents Sea population caused by breeders moulting later than non-breeders (see text).

Table 6.2. Calculated dates (see text) at which juveniles fledged and parents regained flight ability in three populations of barnacle geese *Branta leucopsis*. Statistical significance based on median two-sample tests; n denotes the number of juvenile and adult birds, respectively, for which fledging date and end of wing moult could be calculated.

	Fledging	End of moult	Difference	n	*Z*	*P*
Barents Sea	31 Aug	28 Aug	+3 days	861, 924	6.8359	< 0.0001
Baltic	29 July	8 Aug	-10 days	3 777, 10 493	-45.4520	< 0.0001
North Sea	23 July	3 Aug	-11 days	131, 214	-7.9625	< 0.0001

Food quality

In the Barents Sea population, Nitrogen content of food plants showed a peak around 20 June, c. two to three weeks before hatching (N-content = -29.040 + 0.3767 * date – 0.0011 * date^2; date: $P < 0.0001$, date^2: $P < 0.0001$). In the Baltic, nitrogen content was highest around 20 April, c. five weeks before hatching (N-content = -0.850 + 0.0625 * date – 0.0003 * date^2; date: P = 0.002, date2: P < 0.001). In the North Sea population, no peak in Nitrogen content was apparent, and Nitrogen content declined throughout the season (Breeding site: N-content = 6.073 - 0.0214 * date; date: $P < 0.0001$, date^2: NS; Staging site: N-content = 5.535 - 0.0233 * date; date: $P < 0.0001$, date^2: NS). Presumably, Nitrogen content already had reached its highest value before measurements started in March, at least two months before hatching. Nitrogen content was higher at feeding sites in the study colony compared to a staging site in the North of the Netherlands, where barnacle geese do not breed (Fig. 6.3).

Post-fledgling survival and selection on timing of breeding

In the North Sea and Barents Sea populations, one common resighting probability could be used for all years, whereas in the Baltic resighting probabilities were year-specific (Table 6.3). In the North Sea population, post-fledging survival was very high, on average 97%, and was not related to lay date (ANODEV $P = 0.41$; Table 6.3; Fig. 6.4). In the Baltic and Barents Sea populations, post-fledging survival significantly declined with lay date (ANODEV, $P = 0.006$ and $P = 0.005$, respectively; Table 6.3; Fig. 6.4). In the Baltic, post-fledging survival averaged just over 90%. In the Barents Sea, post-fledging survival was much lower than in the two

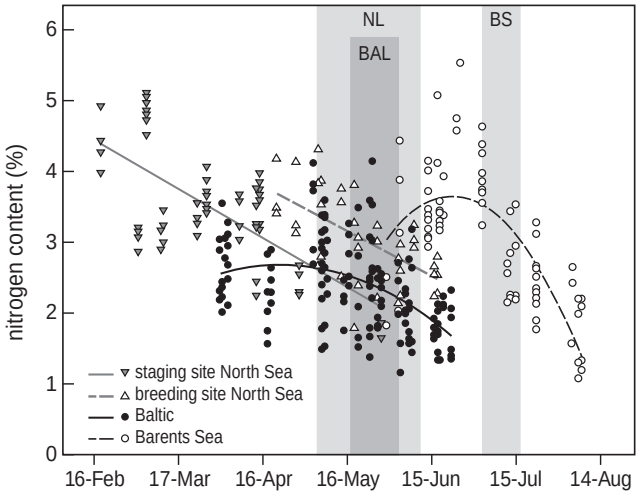

Figure 6.3. Food quality (N content) at staging and breeding sites of the three populations of barnacle goose *Branta leucopsis*. Shaded boxes indicate the periods during which 90% of eggs hatch in the three populations (Dutch = NL, Baltic = BAL, Barents Sea = BS).

Table 6.3. Modelling post-fledging survival in three populations of barnacle geese *Branta leucopsis* using capture-resighting analyses in Program MARK (see text). Φ denotes survival, P resighting rate, a age, and t time. Δ AICc: Difference in the corrected Quasi Akaike's Information Criterion between models. N.P. number of parameters. For each population, the best model is given in bold.

Model name	Δ AICc	Likelihood	N.P.	Deviance
Barents Sea (608 individuals, 3 cohorts)				
Φ(a2*t),P(a2*t)	10.2767	0.0042	11	1994.23
Φ(a2*t),P(..)	4.2845	0.0833	7	1996.40
Φ(a2;a1=laydate),P(..)	0.0000	1.0000	4	1998.19
Φ(a2),P(..)	13.0456	0.0015	3	2013.25
Baltic (956 individuals, 13 cohorts)				
Φ(a2*t),P(a2*t)	1.1090	0.5744	71	11 622.73
Φ(a2*t),P(..)	424.4903	0.0000	38	12 113.67
Φ(a2;a1=laydate,a2=t),P(a2*t)	0.0000	1.0000	57	11 650.39
Φ(a2;a1=constant,a2=t),P(a2*t)	18.4930	0.0000	56	11 670.94
North Sea (105 individuals, 2 cohorts)				
Φ(a2*t),P(a2*t)	6.1809	0.1368	7	190.71
Φ(a2*t),P(..)	3.9490	0.4617	5	192.70
Φ(a2;a1=laydate,),P(..)	1.7944	0.3114	4	192.63
Φ(a2),P(..)	0.0000	1.0000	3	192.91

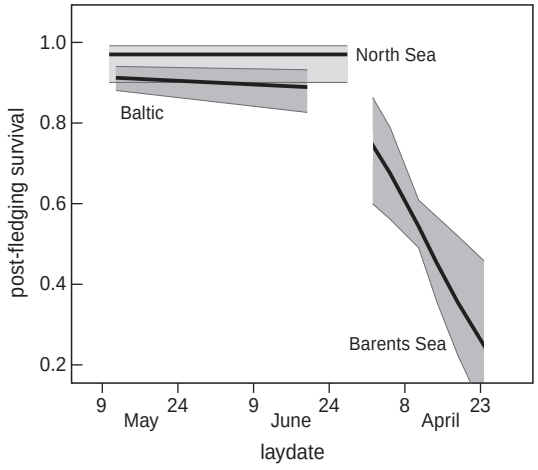

Figure 6.4. Post-fledging survival in three populations of barnacle geese Branta leucopsis in relation to laydate. Bold lines indicate post-fledging survival, shaded areas represent 95% confidence limits. Lines are based on the analyses presented in table 6.3.

temperate populations, averaging 55%. (Fig. 6.4)

We calculated the number of young *per nesting attempt* that arrived at the wintering grounds as outlined in the methods, combining the relationships derived from the survival analyses (Table 6.3; Fig. 6.4) with data on the production of fledged young from the breeding grounds. In the North Sea and Baltic populations, the number of fledged young arriving at the wintering grounds declined linearly with standardized lay date, whereas the relationship between standardized lay date and number of fledged young was quadratic in the Barents Sea population, with most surviving young being produced at intermediate lay dates (Fig. 6.5, Table 6.4). In the North Sea and Baltic populations, most birds started egg laying at the moment when reproductive prospects already had declined, whereas the median date at which birds in the Barents Sea population laid their eggs corresponded well with the date that yielded the highest number of surviving young (Fig. 6.5). Consequently, the standardized selection differential (see methods) was close to zero (0.035) in the Barents Sea population, indicating weak or no (directional) selection on lay date. In the Baltic, and especially the North Sea population, however, there was considerable selection for earlier breeding with standardized selection differentials of -0.305 and -0.663, respectively.

Discussion

Why do temperate-breeding birds breed too late?

We found that recently established temperate populations of barnacle geese have advanced their reproductive season considerably compared to their arctic-breeding conspecifics. However, the advancement of lay and hatch dates was not enough to fully exploit the peak in food quality, which occurs much earlier in the season at lower latitudes. On average, food quality was highest between one and two months before hatching, and newly hatched chicks in the Baltic were confronted with a food supply that was c. 40% lower in quality compared to the food of chicks hatched in the Arctic, where hatching closely approaches the peak in food quality (Fig. 6.3). Food quality during hatching in the North Sea population, although already declining from the spring peak, was comparable to that in the Arctic. However, the nitrogen contents of food plants at our study site were unusually high due to the management features of this reclaimed area, and are not typical for more representative sites at this latitude (e.g. compare the staging site in Fig. 6.3). Food quality, measured as the nitrogen content of forage plants, is an important determinant of gosling growth and survival (Larsson and Forslund 1991; Cooch et al. 1991; Larsson et al. 1998) and nitrogen content of forage plants can serve as an index of the high-quality food needed for gosling growth.

In contrast to the close match in the Barents Sea population, the median standardized lay date for both temperate populations (Baltic and North Sea) occurs at the time well beyond the point where the mean number of surviving young per nest is at its maximum. The compound effect of brood size at hatch and survival of

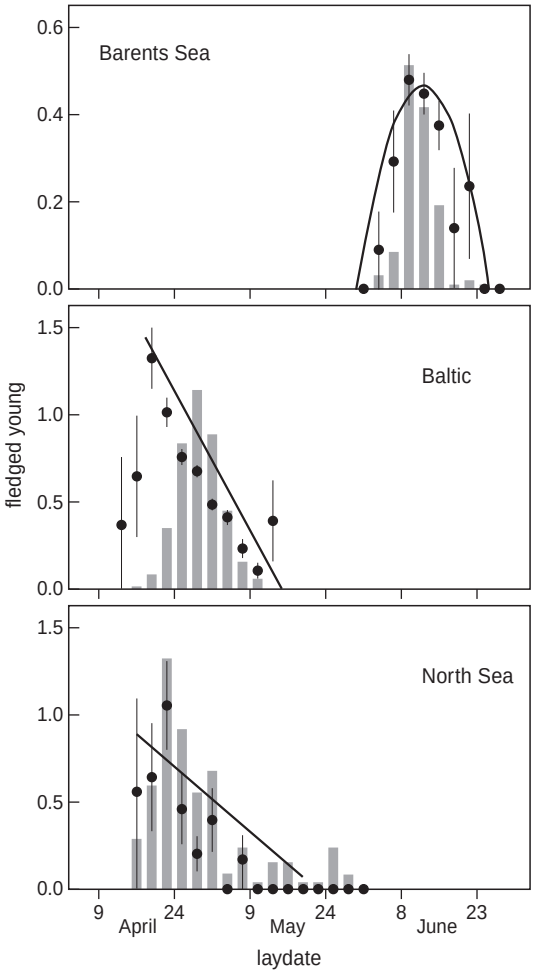

Figure 6.5. Timing of reproduction in relation to fitness in three populations of barnacle geese *Branta leucopsis*. Black dots indicate the number of fledged young per nesting attempt surviving to arrival on the wintering grounds in their first winter (means for three-day intervals), regression lines are based on the analyses presented in table 6.4. Grey bars indicate the frequency of lay dates observed in each population.

Table 6.4. The effect of laydate on the number of young per nesting attempt arriving at the wintering grounds, using linear regression. When laydate^2 was not significant it was removed from the model, and the remaining linear relationship indicates directional selection on laydate. Where laydate^2 is significant, the relationship is quadratic, indicating stabilizing selection on laydate.

	Laydate			Laydate^2			
	estimate	t	P	estimate	t	P	N
Barents Sea	0.380	2.50	0.01	-0.003	-2.56	0.01	347
Baltic	-0.053	-11.52	<0.0001	0.000	0.72	NS	3 423
North Sea	-0.025	-2.77	0.006	0.000	0.39	NS	136

goslings until fledging, based on observation of family size of marked parents with known laying dates, modulated by post-fledging survival is assembled in Fig. 6.5 and is our crown witness regarding these lay date effects on fitness. As a result of these effects, selection on lay date was stabilizing in the Arctic, whereas there was strong directional selection for earlier breeding in the Baltic and North Sea populations.

Despite this fitness penalty in the timing of breeding in the Baltic and North Sea populations the temperate populations achieve a higher output of fledged young per nesting female that reach the wintering grounds in October-November compared to the Barents Sea population (Barents Sea: 0.42 (n = 347); Baltic: 0.71 (n = 3.423); North Sea: 0.51 (n = 136). Owen and Black (1989) reported data for the Spitsbergen-breeding population of the barnacle goose on survival of juveniles ringed near fledging on the breeding grounds that were observed in Scotland the following winter. Survival in six "normal" seasons (ranging from 1977 through 1984) varied little (mean 0.84) but in 1986 (a late season) this value fell to 0.65. Barents Sea birds thus experience a higher mortality (mean survival 0.55) during autumn migration, presumably reflecting the impact of the fall hunt during the first lap of their journey in Russia. This mortality figure is virtually identical to that reported by Menu et al. (2005) for juvenile greater snow geese *Chen caerulescens atlantica* on their 5-week 3000 km fall migration from the high arctic breeding site to the St Lawrence in Quebec (0.55 on the basis of sightings of neck-banded parents with goslings before and after, 0.59 mean for five seasons from a banding campaign at both sites). Hunting kill by native people is included, but believed to be low.

Clutch size generally declines with lay date in avian populations that breed in seasonal environments due to a decline in offspring value and an effect of condition, with birds in poorer condition both producing smaller clutches *and* laying later (Klomp 1970; Drent and Daan 1980; Hochachka 1990; Daan et al. 1990). In arctic-breeding geese, the seasonal decline in clutch size is particularly strong (Lepage et al. 1999; Lepage et al. 2000; Bêty et al. 2003), and clutch size indeed declined strongly in all of our study populations (own observations). Both hatching success and pre-fledging survival frequently show highest values at intermediate lay dates in arctic geese and other waterfowl (Findlay and Cooke 1982; Brinkhof et al. 1993; Lepage et al. 2000), probably due to higher predation when newly hatched chicks are relatively rare at the start and towards the end of the total hatching period (Lepage et al. 2000). Post-fledging survival and recruitment generally decline with lay date in many bird species (Nur 1990; Brinkhof et al. 1993; Verhulst et al. 1995). In our study populations, post-fledging survival of individual goslings declined steeply with date in the Barents Sea population, moderately in the Baltic, and not in the North Sea population.

The combined outcome of these effects usually is a decline in fitness with lay date, with the majority of the population laying too late (Lack 1968; Price and Liou 1989). This is what we also found in the Baltic and North Sea populations. Since barnacle geese have only recently colonized temperate environments, it is possible that they have not yet been able to adapt fully to the earlier springs at these latitudes, and therefore currently lag behind. Adaptation can occur as a result of

phenotypic plasticity or through a micro-evolutionary response to directional selection on lay date (Visser 2008). In the Baltic, population mean lay date has indeed advanced between 1985 and 2004 (Fig. 6.6A; $R = –0.47$ $P < 0.05$). However, during the same period it has become warmer. We examined change in lay date in relation to spring phenology by employing "growing degree days" (GDD) from January through April, a frequently used measure in studies of spring phenology (Botta et al. 2000). GDD explained over 80% of the variation in lay date (Fig. 6.6B; R = –0.90 P < 0.0001), and GDD increased over time ($R = 0.45$ $P < 0.05$). Hence, much of the observed advancement in lay date could be attributed to warmer springs. Shifts in lay date have been observed in many other bird species (Crick et al. 1997; McCleery and Perrins, 1998), and most likely result from phenotypic plasticity, but do not necessarily mean that birds are perfectly adapting to the warming climate (Visser 2008). After correcting for the effect of global warming, the remaining advancement in lay date was reduced to three days (Fig. 6.6C; $R = –0.58$ $P = 0.01$). However, this advancement in laydate could easily be explained by the changed age-distribution of the breeding birds, as there are strong age-effects on lay date (Forslund and Larsson 1992), and does not have to be the result of an adaptation, by whatever mechanism, to the earlier springs that occur at temperate latitudes compared to those in the arctic. In fact, directional selection on lay date is increasing, as can be seen from the increasingly negative standardized selection differentials (Fig. 6.6D; $R = –0.60$ $P = 0.01$). Hence, the rate of adaptation, if any, in the Baltic population is insufficient to keep up with earlier springs. Similar results have been found for great tits *Parus major* (Visser et al. 1998) and pied flycatchers F*icedula hypoleuca* (Both and Visser 2001) breeding in the Netherlands.

There are several explanations to why the majority of individuals in avian populations fail to breed in time. The most relevant one here is the "constraint hypothesis" (Lack 1966; Perrins 1970; Nager et al. 2000), which revolves around the idea that only a minority of females is able to monopolize the limited amount of food early in spring and can thereby reach a nutritional state that is needed for egg production sufficiently early in the season, whereas most females are constrained and forced to delay their breeding until after the best time for offspring rearing. We believe that a similar reasoning can explain the fact that the recently established southern populations of the barnacle goose that we studied breed too late and, as yet, have failed to evolve towards the optimal timing of breeding.

In the Barents Sea population, we found that lay date was optimal with respect to parental fitness, as suggested in other high-arctic nesting geese (Lepage et al. 2000; Black et al. 2007). Why do arctic-breeding geese seem to be able to breed in time, whereas their temperate conspecifics fail to do so? Arctic-breeding geese and other herbivorous waterfowl travel along a climatic gradient during spring migration to their northern breeding sites, thereby taking advantage of the spring flush of forage plants at each stopover site. This idea is formally known as “the green wave hypothesis” (Drent et al. 1978; Owen 1980). It enables the birds to exploit the early spring growth along the flyway and gradually accumulate body stores from the food they encounter at each site (Madsen and Klaassen 2006). When they finally arrive

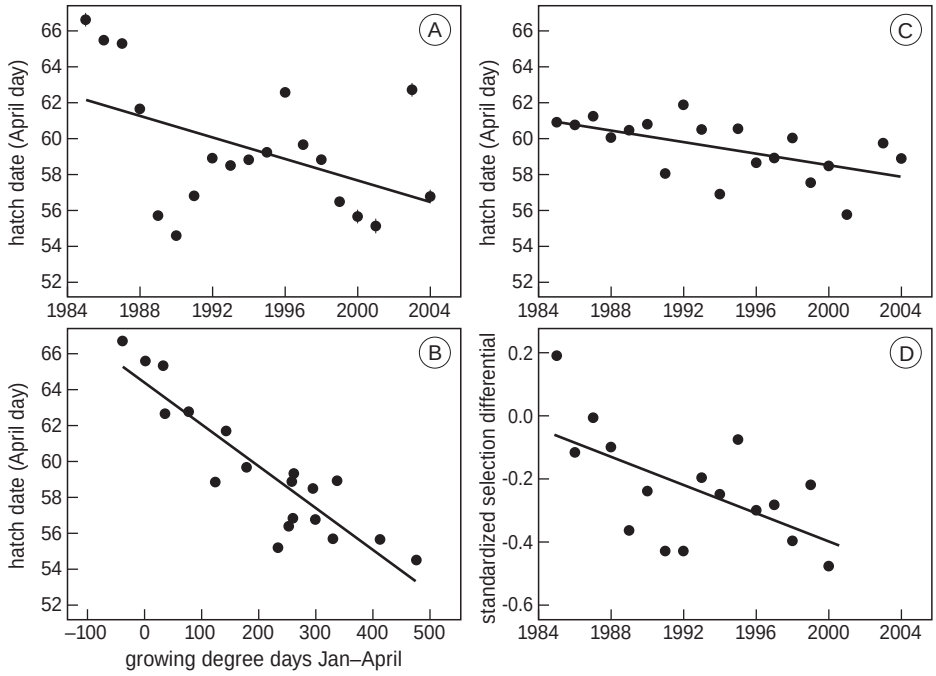

Figure 6.6. Annual variation in mean hatch date in the Baltic population of barnacle geese *Branta leucopsis*. A: Population mean hatch dates (bars denote standard errors) between 1984 and 2004. Hatch date advanced by c. 6 days during the 20 year study period. B. Population mean hatch dates as a function of the number of growing degree days (see text). Birds lay earlier following warm winter and springs. C: Population mean hatch dates between 1984 and 2004 corrected for the effect of growing degree days. Corrected hatch date advanced by c. 3 days during the 20 year study period. D. Annual standardized selection differentials (see text) increased indicating increasing selection for earlier breeding during the study period.

in their arctic breeding grounds, they are ahead of the wave of grass growth and are forced to draw, at least partly, on their capital of stored resources for egg formation, enabling them to breed earlier and allocate more of the local resources to the growth of their young. Studies using stable isotopes indeed showed that arctic-breeding geese often use a mixed capital/income breeding strategy (Drent et al. 2006). Results from tracking studies in six goose species also underline the conclusion that egg formation commences along the flyway before arrival at the nesting colony (Drent et al. 2007). Temperate-breeding birds do not have this advantage of exploiting successive waves of spring growth, forcing them to postpone breeding until adequate condition is gained from local resources. For avian herbivores that rely on a seasonal food source, travelling to the Arctic may therefore be an evolutionary escape from the problem that many temperate-breeding birds face: how to time the breeding season in relation to the peak in food supply?

Why do temperate-breeding birds not moult earlier?

Timing of wing moult differed much less between populations compared to timing of reproduction, resulting in a larger time gap between hatching and the start of wing moult in temperate populations. We found that barnacle geese in the Barents Sea population that were leading young postponed the start of wing moult by c. two weeks compared to non-breeders. Such a difference was absent in temperate populations. Still, compared to their temperate-breeding counterparts, arctic-breeding barnacle geese have only one third of the time between hatching and start of wing moult. Hence, the time window during which parents can replenish reserves lost during incubation before undergoing moult of wing feathers is much longer in temperate-breeding birds (see also Loonen et al. 1997). Temperate-breeding birds might also be forced to postpone the start of parental wing moult relative to the timing of hatching due to the lower food quality that birds encounter after hatching in the North Sea and Baltic populations. Indeed, Van der Jeugd et al. (2003) showed that birds in the Barents Sea population were significantly heavier at the start of wing moult compared to Baltic birds. Finally, timing of wing moult has also been shown to be under strong genetic control in barnacle geese (Larsson 1996), and therefore timing of wing moult might be slower to evolve than lay date.

Juveniles fledged almost two weeks before their parents regained flight ability in the North Sea and Baltic populations. In the Barents Sea population, the date at which juveniles fledged was very close to the date at which parents could fly. Hence, the synchronisation between wing moult and fledging has broken down in temperate populations. We do not know whether this represents a cost to parents or young, although we frequently observed that young would fly away from their parents during disturbances and predator attacks at both temperate study sites.

Explaining the recent range expansion

Barnacle geese expanded their breeding range during a period when the population increased twenty-fold. It is likely that the same factors that led to the increase of the population were also responsible for the establishment of temperate-breeding colonies. A combination of improved feeding conditions due to changes in agricultural practice in the wintering areas (Van Eerden et al. 1996; Abraham et al. 2005; Gauthier et al. 2005; Fox et al. 2005; Van Eerden et al. 2005) and reduced prosecution which lead to reduced mortality and disturbance (Ebbinge 1991) are the main factors held responsible for the increase in many populations of waterfowl in the northern hemisphere. At the same time, these changes will have led to a situation where geese now are able to reach adequate breeding conditions earlier in the season which enables them to produce a clutch and incubate it successfully at lower latitudes. Increasing density-dependent effects in the traditional breeding grounds due to the growing population might be an additional factor that triggered birds to seek greener pastures (Van der Graaf et al. 2006a). However, this can hardly explain the launch of the Baltic breeding population that already took place in 1971 when population levels were still low. Van der Graaf et al. (2006a) could not find any direct indications that changes in land use in the Baltic might explain the establishment of the Baltic population, although breeding in the Netherlands very likely was

influenced by such changes. The difference in food quality between our study site in the Southwest of the Netherlands, where the majority of the North Sea population breeds, and a spring staging site in the North of the Netherlands where breeding birds are absent, underlines the importance of local food quality (Fig. 6.3). The juxtaposition of rich soils and brackish water in the reclaimed area in the SW Netherlands combined with summer grazing by livestock contribute to the high food quality there (Vulink 2001).

All recently established breeding areas are situated within the barnacle goose flyway, i.e. they are confined to historical wintering areas and staging grounds of the species. Prior knowledge of potential breeding areas therefore seems to be important for the species. Although the breeding population in the traditional breeding area has extended its range with increasing densities, there seems still ample suitable breeding habitat vacant (Kalyakin 1986; Kalyakin 2001). Interestingly, no eastward expansion has been reported so far (but see Pokrovskaya and Gavrilo 1998). Syroechkovsky Jr. (1995) even speculates that the westward expansion within the Russian Arctic observed during the last two decades could be in fact a re-colonization of former breeding sites. Taking this idea further one might also ask whether the temperate sites were in fact part of the species' breeding distribution in historical times, or, even pre-historical times (Ploeger 1968). Due to the exceptional vulnerability of geese and other waterfowl during the flightless period, they would then have become extinct when the human population increased. Unfortunately, to our knowledge, no information is available to test this idea.

Conclusions

Temperate-breeding populations of barnacle geese, which have been established recently, are seemingly not completely adapted to the environmental circumstances that prevail at low latitudes. Nevertheless, absolute fitness and, hence, population growth rate in at least the North Sea population is higher than that for the Arctic population as a whole. However, it is not possible to compare absolute fitness between a recently-established population and an older one because of very strong density dependent effects (Larsson and Forslund 1994). Reproductive output and survival of the Baltic population was initially very high as well, but has now been greatly reduced to levels where the population is actually declining (Larsson unpublished). Low food quality and high levels of predation by red foxes *Vulpes vulpes* and the recently re-established white-tailed eagle *Haliaetus albicilla* are the main reasons for the recent population decline. During the 1970s and 1980s, when most temperate barnacle goose populations were established, predators were still relatively rare (as a result of widespread use of pesticides and prosecution) and this predator-lull might well have facilitated their initial success.

Intriguingly, another goose species of which the historical range has included temperate areas for a much longer period of time (Madsen et al. 1999), the greylag goose *Anser anser*, is capable of breeding sufficiently early. In this species, eggs hatch already in March, when food quality is still high (Kamp and Preuss 2005). They owe this to a combination of a broader diet, which makes them less

dependent on a single food-peak (Amat 1995), and their larger body-size, which enables them to produce a full clutch from body stores and thus makes them less dependent on exogenous food sources (Klaassen et al. 2006b). Their larger body size compared to arctic-breeding geese they most probably owe to relaxed selection on offspring growth and final size due to the longer breeding season (Dunn and MacInnes 1987). Successful adaptation to early springs in temperate barnacle geese therefore most probably requires an evolution towards larger body size (as has been the case in the Canada goose complex, see Dunn and MacInnes 1987; Paxinos et al. 2001), paving the way for a shift in breeding time. At present, birds in the relatively young North Sea population are indeed largest (own obs.). However, despite strong selection on body size, body size actually declined in the Baltic due to overruling phenotypic effects of increasing population density (Larsson et al. 1998), possibly masking the evolution of body size itself (Merilä et al. 2001).

The observed mismatch between reproduction and food supply in temperate regions is highly relevant in the light of global change. Global temperatures are predicted to increase, and the increase is predicted to be most extreme in arctic areas (IPCC 2001). This would mean that, in line with our results for temperate populations, barnacle geese as well as other arctic-breeding geese will be confronted with much earlier springs also at higher latitudes, and they might not be able to keep up with this shift on the short term.

Acknowledgements

This study is the result of the combined effort, vision and long-term engagement of many people and institutes. We want to thank Lars Gustafsson and especially Pär Forslund (Uppsala University) for their part in the early years of the study of the Baltic population. Some 40 people, too many to mention here, took part in collecting the field data in this long-term study. Mennobart van Eerden (RIZA, Lelystad) paved our way to research in the arctic by suggesting the Kolokolkova Bay in the Russian Federation as an ideal study-site to set up our companion long-term population study, and led our first expedition there. The support of the Institute of Biology in Syktyvkar, the administration of the Nenets Autonomous District in Nar'yan Mar, the State Nature reserve Nenetskiy, Nar'yan Mar, and the Russian Hunters Association for the studies in Russia is gratefully acknowledged. The study at Hellegatsplaten, The Netherlands, was possible due to support of the owner, Staatsbosbeheer. Almost 1,000 volunteer ringreaders contributed their observations of marked barnacle geese. During the first eight years, these observations were gathered and processed by Bart Ebbinge and Jan Burgers. Financial assistance came from The Swedish Natural Science Research Council (grants to KL), the Swedish Environmental Protection Agency, Olle och Signhild Engkvist Stiftelser, the Royal Swedish Academy of Sciences, the Swedish Foundation for International Cooperation in Research and Higher Education (grant to HJ), the Netherlands Arctic Program of the Netherlands Organisation of Scientific Research (NWO), the Partners for Water PRISM project (Netherlands-Russian cooperation), the Danish Forest and Nature Agency (grants to RD),the BIRD program of the European Science Foundation, the University of Groningen and the Faunafonds. GE was supported by scholarships from the 'Marianne und Dr. Fritz Walther-Fischer Stiftung', Germany, and the 'Ubbo Emmius Programme' at the University of Groningen. JS acknowledges financial support of the Deutsche Forschungsgemeinschaft (DFG).

Box

C

Nest attentiveness in temperate and arctic-breeding barnacle geese

Götz Eichhorn
Julia Karagicheva

In barnacle geese like in most waterfowl incubation is carried out solely by the female. In contrast to eiders *Somateria molissima* and some of the larger waterfowl species (Afton and Paulus 1992) female barnacle geese cannot sustain themselves through incubation by drawing from body stores alone, but rely on additional nutrient input from feeding recesses. Incubation behaviour is expected to be regulated by body condition as well as by environmental factors, among them weather and food conditions and predation pressure (e.g., Thompson and Raveling 1987; Poussart et al. 2001; Poisbleau et al. 2007). At least some of these conditions are further expected to differ for birds from the long-distance migratory population of barnacle geese breeding in the Russian Arctic and birds from the sedentary population breeding in the Netherlands. Here we describe incubation patterns (in more detail for the Dutch birds) and compare nest attentiveness of females from these two study populations. We were further interested in how incubation behaviour relates to the different use of body stores found for females from these populations (ch. 7 this thesis).

Methods

Temperate-breeding barnacle geese from the North Sea population were studied in the Netherlands at Hellegatsplaten (51°42'N, 4°20'E), one of the largest colonies in the Delta area in the southwest of the country. Arctic-breeding barnacle geese from the Barents Sea population were studied in a colony on the northwest coast of Kolokolkova Bay, near the abandoned settlement of Tobseda, northern Russia (68°35'N, 52°20'E). Details on these study populations and study sites can be found in the introduction of this thesis.

To monitor incubation behaviour of females from the Dutch population a temperature probe (5 mm in diameter, 10 to 20 mm long) was installed in the bottom of the nest cup between the eggs, so that it pointed upwards with the end at level of the upper egg surface. Data were recorded at 30 sec intervals and logged

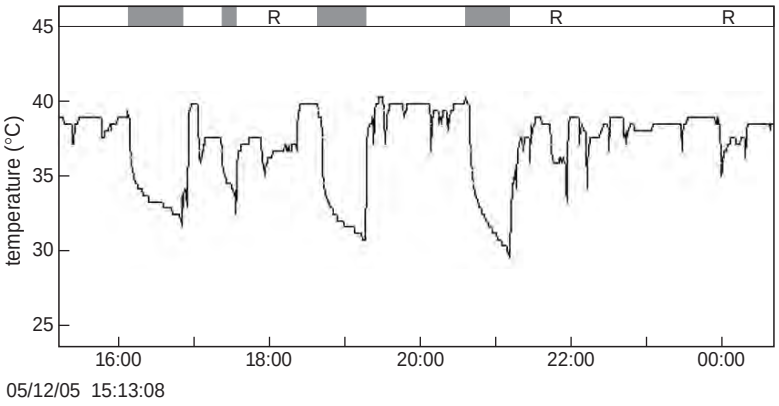

Figure BoxC.1. Example of temperature readings measured at 30 sec intervals with probes installed in the nest of incubating female barnacle geese from the Dutch study population. Four recesses (between 16:00 and 24:00) can be detected (marked by bars; R= resettling on the clutch without leaving nest).

onto HOBO loggers (Onset Computer Corporation, model H08-008-04 or H08-031-08). With this method 14 nests were monitored on 4 to 18 days (average 10 days) during incubation in 2005 (12 nests hatched, 2 females abandoned the nest before, likely due to human interference). Incubation and recess bouts were read from temperature graphs displayed by the software programme BoxCar Pro 4 (see Fig. BoxC.1 for an example). The interpretation of graphs was calibrated by comparing temperature logger data with simultaneous direct observations. Displacement of the probe by the bird happened in a number of nests for part of the measurement period resulting in irregular temperature graphs. Such periods as well as readings around the time of hatching were discarded. On days when geese left the nest due to human interference (e.g., during weekly data download) the data of that whole day were discarded. For data from the Dutch population we included only data that comprised complete 24 hour periods to calculate the following three parameters: *daily recess frequency* (i.e., number of recesses per 24 hours), *recess duration* (which was averaged per female before calculation of the mean over all females per day) and *total daily recess time*.

Data on females from the Russian population were gathered by direct observation (Karagicheva and Gurtovaya in prep.). Individual nests were scanned using binoculars and a 30–40x telescope at frequent intervals (usually every 10–15 minutes) and female presence/absence on the nest was noted. In total 42 nests were monitored in 2004 and 2005 from a permanent hide erected on a dune overlooking the colony. All nests were marked by flagged stakes visible from the hide. Single observational bouts lasted from 6 to 48 hours and covered all periods of the day and stages of incubation. Laying dates, clutch size and hatching success were determined by nest checks every 1–2 days.

Average start of incubation in the sample of 14 females from the Dutch population was 30 April. For birds from the Russian study site start of incubation peaked on 9 June in 2005 for the colony as a whole. These dates were either back-calculated from hatching date or, alternatively, from dates of egg-laying assuming commencement of incubation at the 3rd egg-stage (for clutches of 3 to 5 eggs) or 4th egg-stage (for clutches larger than 5 eggs) and 33 hours laying interval (Alisauskas and Ankney 1992a; Schubert and Cooke 1993). Incubation in barnacle geese lasts for approximately 25 (24–26) days (Dalhaug et al. 1996; own obs.). To give an indication of the ambient temperatures experienced by females from both populations during incubation we plotted data of daily maximum, mean and minimum temperatures for a period of 30 days starting from the abovementioned average dates of incubation initiation. At the Russian field site temperature was measured adjacent to the colony. Data provided from the Royal Netherlands Meteorological Institute (KNMI) for the weather station in Vlissingen (51° 27' N, 03° 36' E) were taken as representative for the Dutch breeding site. Temperature sensors at both sites were installed at 2 m and 1.5 m above ground, respectively, and protected from sun radiation. An estimate of the lower critical temperature in the barnacle goose was calculated after Calder and King (1974) yielding 4°C (for 1660 g body mass at mid incubation). However, Stahl (2001) reported a value of 12°C for this species, and we assume the true value within the range of these two estimates.

Results

Incubating females from the Dutch colony left the nest on average 2.6 times per day for a mean period of 30 minutes per recess; the accumulated recess time per day was 78 min translating to a nest attentiveness of nearly 95% (Table BoxC.1). When related to day of incubation recess frequency showed no clear trend for most of the incubation period, but decreased over the last three days of incubation, whereas duration of recesses remained stable over the same period. Recess bouts appeared to be shorter during the first six days of incubation (Fig. BoxC.2).

Daily recess time of females from the Arctic Russian colony was higher than for Dutch birds for most of the incubation period (Fig. BoxC.3) and averaging 157 min over 26 days of incubation (equating to a nest attentiveness of 89%). As in Dutch breeders Russian birds reduced their time off the nest over the last three days of incubation. Thus, daily recess time was reasonably stable over the first 22 days of

Table BoxC.1. Incubation rhythm in the barnacle goose from a Dutch colony.

	Mean ± SE	n	Range
Daily recess frequency	2.6 ± 0.1	138	0 - 6
Recess duration [min]	30.3 ± 1.3	134	9 - 99
Daily recess time [min]	77.6 ± 3.7	138	0 - 214
Daily nest attentiveness [%]	94.6 ± 0.3	138	85.1 - 100

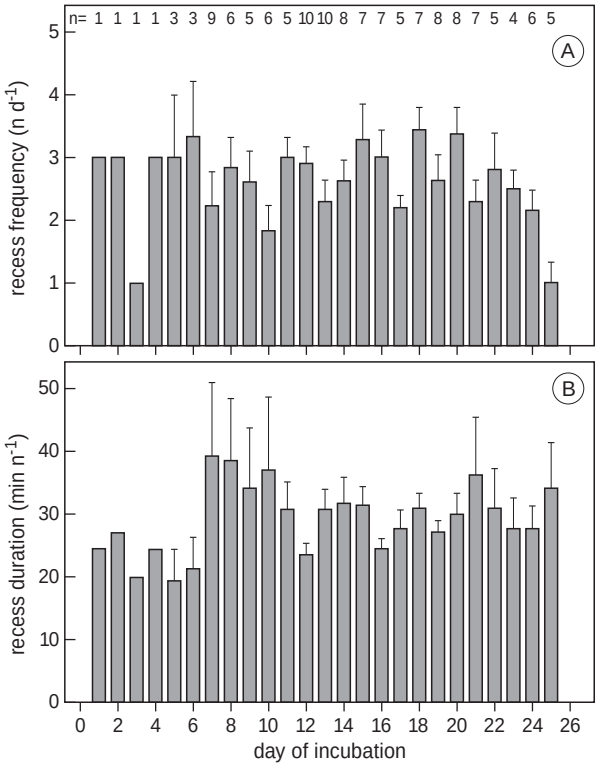

Figure BoxC.2. Pattern of daily incubation recesses for female barnacle geese from a Dutch breeding population. A) Mean ± SE recess frequency and B) recess duration calculated from daily means of individual females. Number of females monitored per day is given at the top (n = 138 bird-days in total).

incubation averaging 80 min and 177 min in Dutch and Russian birds, respectively. Despite the paucity of our observations on the Dutch birds, actual daily feeding time differs even more than the recess times indicate. The proportion of time spent feeding during a recess (head below horizontal and grazing or seeking for food) amounted to 64 ± 4% (mean ± SE, n = 11) and 77 ± 2% (n = 34) for Dutch (in 2005) and Russian (2003 and 2004 combined) breeders, respectively. Thus, estimated average daily feeding time for Dutch incubating females (50 min) would be only 40% as long as compared to their Russian conspecifics (121 min).

Discussion

Studies on Canada geese *Branta canadensis moffitti* (Aldrich and Raveling 1983), greater snow geese *Anser caerulescens atlanticus* (Poussart et al. 2001) and black brent *Branta bernicla nigricans* (Eichholz and Sedinger 1999) reported an increase in daily recess time as incubation progressed, whereas studies on emperor geese *Anser canagicus* (Thompson and Raveling 1987), brent geese *Branta b. bernicla* (Spaans et

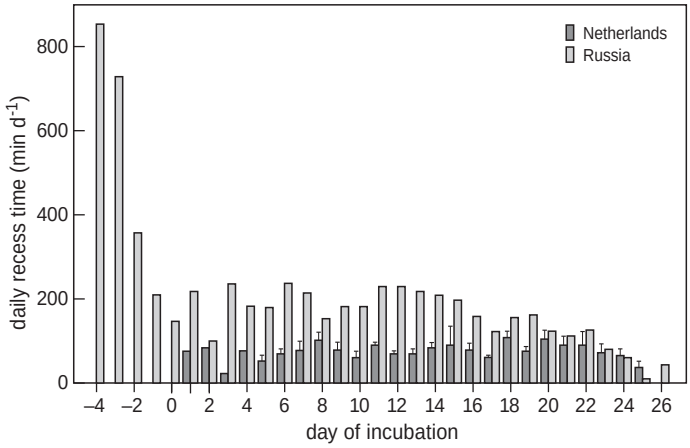

Figure BoxC.3. Average daily recess time per day of incubation for female barnacle geese from a colony in the Netherlands and Arctic Russia. For Dutch birds standard errors are given based on the sample of birds monitored with help of temperature loggers installed in the nest (n per day given in Fig. 1A). For Russian birds only averages are shown from direct scan sampling procedures of 42 nests in 2004 and 2005 combined.

al. 2007) and barnacle geese (this study) did not find such a trend. However, all studies observed increased nest attendance during the last few days of incubation. Weather conditions and predation pressure have been suggested as important environmental factors regulating incubation behaviour in geese (Aldrich and Raveling 1983; Thompson and Raveling 1987; Poussart et al. 2001; Poisbleau et al. 2007). Weather and food conditions generally improve over the season and may stimulate absence from the nest. In contrary, unprofitable feeding conditions may cause unexpected high nest attentiveness (Jonsson et al. 2007).

Barnacle geese from the Dutch colony enjoy milder temperatures than geese breeding in the Russian Arctic (Fig. BoxC.4) thereby likely reducing costs for both maintaining body temperature and reheating the clutch after incubation recesses. Feeding conditions, as judged by the nitrogen content of food plants, appeared to be comparable for Dutch and Russian barnacle geese (ch. 6 this thesis), and predation pressure on unattended clutches seemed to be actually lower in the Dutch colonies (own obs.). Thus, the above cited environmental factors can hardly explain the higher nest attendance of geese from the Dutch colony. The finding of a higher nest attentiveness in temperate compared to arctic-nesting barnacle geese is supported by other studies. Tombre and Erikstad (1996) reported for barnacle geese from the Spitsbergen population an average daily recess time of 151 minutes (N = 76 nests observed at Ny-Ålesund) with 7.2 recesses per day lasting 21.5 minutes on average. This daily nest attendance of 89.5% contrasts with 94.8% found for free-flying barnacle geese breeding at the Wildfowl Trust's reserve at Slimbridge, UK (Lessells et al. 1979; Afton and Paulus 1992).

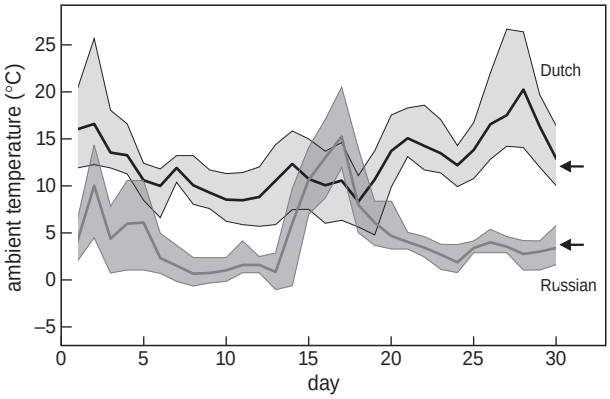

Figure BoxC.4. Daily maximum, mean and minimum temperatures measured at the Dutch and Russian study sites in 2005 for a period of 30 days starting from the respective mean dates of start of incubation (30 April and 9 June). The arrows at the right mark two estimates of the lower critical temperature (see methods for details).

Apart from external factors females adjust incubation behaviour in relation to the state of body stores (see discussion in ch. 7). They may balance their stores in order to not exhaust them completely until hatch. Female Spitsbergen barnacle geese with experimentally prolonged incubation (extra 5 d by clutch swap) although sacrificing body condition did not increase recess time in late incubation (Tombre and Erikstad 1996). However, with an estimated 32 g fat residue at hatch and a daily fat loss of 10 g the Russian female barnacle geese are apparently unable to incubate for another 5 days unless they notably increase their food uptake (ch. 7).

In conclusion, temperate barnacle geese commence incubation with more body stores allowing them to reduce feeding time compared to arctic conspecifics (see also Table 7.5 in ch. 7). Apparently, nest attentiveness is maximised as permitted by the amount of body stores, even under actually benign environmental conditions (including relaxed predation pressure in the absence of foxes).

Chapter 7

Fuelling reproduction: differential use of endogenous nutrient reserves in arctic and temperate-breeding barnacle geese

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Submitted

Abstract

We compared use of endogenous nutrient reserves in breeding barnacle geese *Branta leucopsis* from traditional arctic colonies in the Barents Sea (BS) and recently established temperate-breeding colonies in the Baltic (BAL) and the Netherlands (NL) by studying clutch and egg size, female body mass (BM) loss and the use of fat and protein stores during incubation. Clutch size increases from North to South from 4 to 5 eggs. Average daily BM loss was almost identical in the two temperate populations amounting to 17.0 and 16.5 g in BAL and NL, respectively, whereas arctic-breeding females from BS reduced the loss significantly to 10.6 g d^{-1}. Temperate breeders initiated incubation with 125 g higher BM than arctic females (1742 g at start of incubation) but after 25 days (the average incubation period for this species) BM was similar among the three populations, averaging 1458 g. Female BM loss until the end of incubation (day 25) amounted to 23% (NL), 22% (BAL) and 15% (BS) of the body weight at the start of incubation. Clutch size, laying date and year showed no significant effect on BM during incubation. By means of deuterium isotope dilution we estimated fat mass (FM) and fat-free mass (FFM) in a sub-sample of females (incubating day 2 to 21) from the NL and BS populations. NL birds had consistently higher fat reserves (65 g on average) than BS birds. However, females from both populations showed a similar rate of FM loss (9.4 g d^{-1}) during incubation. In contrast, FFM was lost at 9.3 g d^{-1} in NL birds but only at a non-significant rate of 1.5 g d^{-1} in BS birds. Accordingly, somatic lipids accounted for 50% and 86% of female BM loss in the NL and BS population, respectively. The respective energy contents of 1 g utilised BM were 21.1 kJ (NL) and 34.9 kJ (BS) which amounts to 376 and 415 kJ d^{-1} drawn from stored energy in NL and BS birds, respectively. Given their level of lipid stores, the higher depletion of somatic protein in temperate-breeding females cannot be caused by energetic demands. Apparently, the temperate birds accept a higher loss of their protein pool perhaps related to relatively delayed moult. The arctic birds face a shorter recovery period before entering moult and must rebuild body stores in preparation for long-distance migration.

Introduction

Evidence for the adaptive significance of somatic nutrient reserves for successful reproduction has been adduced for numerous species of waterfowl (Alisauskas and Ankney 1992a; Afton and Paulus 1992; Arzel et al. 2006). In particular females of arctic-nesting geese, which usually start nesting when local food resources are still scarce, depend on nutrients deposited earlier along the flyway (notably stores of fat and protein) in order to meet requirements for clutch production and incubation (Gauthier et al. 2003; Klaassen et al. 2006b; Schmutz et al. 2006; Drent et al. 2007). Consequently, the amount of nutrient reserves available at laying has been suggested as the primary proximate determinant of clutch size for these birds (Ryder 1970; Ankney and MacInnes 1978; Alisauskas and Ankney 1992a).

In addition to egg production, body reserves are also needed for incubation, and, in some of the northern geese, these stores represent virtually the only energy supply for the female during the entire period (Thompson and Raveling 1987; Spaans et al. 1999; Bolduc and Guillemette 2003). However, female body mass loss during incubation can vary considerably among waterfowl ranging from 3-33% among 24 anatid species with female-only incubation (Afton and Paulus 1992). Furthermore, since females, at the time of egg laying, are unable to predict the breeding conditions they meet later in the reproductive cycle, some reserves have to be retained at the end of laying as a buffer against unpredictable extra nutrient needs (Tombre and Erikstad 1996; Erikstad et al. 1998). Because of these multiple demands, the allocation of body stores to different stages of the reproductive cycle is subject to trade-offs (Gloutney and Clark 1991; Erikstad et al. 1993; Erikstad and Tveraa 1995).

A consequence of insufficient body reserves may be that females, even if not forced to abandon the nest, must take more feeding recesses during incubation (Aldrich and Raveling 1983; Swennen et al. 1993), which can increase the risk of egg predation and increase the length of the incubation period (Aldrich and Raveling 1983; Thompson and Raveling 1987; Tombre and Erikstad 1996). Demands of laying and incubating eggs can affect parental fitness (Monaghan and Nager 1997). Thus, the trade-off between current and future reproduction may be another factor influencing to what extent body stores will be depleted (Stearns 1992; Erikstad et al. 1998). Some studies in which the incubation period was experimentally prolonged did indeed report negative effects on survival and future fecundity (Lessells 1986; but see Tombre and Erikstad 1996; Hanssen et al. 2005).

In order to verify and better understand the different tactics of reproduction evolved in waterfowl, intra-specific studies of nutrient-stores use among populations breeding in different environments are necessary but scarcely conducted so far (Alisauskas and Ankney 1992a; Rohwer 1992; Esler et al. 2001). For example, there is ample reason to speculate that temperate-breeding geese might make other decisions when allocating body reserves to different stages of the breeding cycle than arctic-breeding populations. The amount of body reserves a female has at the start of egg laying is determined by both the amount of reserves she is able to carry from

the staging areas (Ryder 1970; Ankney and MacInnes 1978), as well as by the amount of food available upon her arrival (Prop and de Vries 1993; Choiniere and Gauthier 1995; Ganter and Cooke 1996). Temperate-breeding geese might have an advantage over their arctic counterparts in this respect, since they have both shorter migration routes and experience more favourable conditions upon egg laying. Furthermore, since the breeding season is more prolonged further south, the time to replenish lost reserves is longer in southern populations, which might be a further advantage. Finally, differences in thermoregulatory costs and predation risk between arctic and temperate populations might also contribute to the extent at which body stores will be depleted.

It is our aim to verify such predictions for arctic and temperate-breeding populations of the barnacle goose *Branta leucopsis*. This species established temperate breeding colonies only about 3 decades ago, and the question how a traditionally arctic-breeding species could successfully adopt a temperate breeding strategy during such a short time span is intriguing (see also chapter 6 in this thesis). Here, we compare the amount of body reserves at the start of incubation as well as the rate with which these reserves are depleted during incubation between two temperate and one arctic population. We will show that large differences exist that invite speculation.

Methods

Study populations

Body mass loss was studied in three recently established populations of the barnacle goose, one arctic and two temperate (Fig. 7.1). In the ancestral Barents Sea population (BS), a colony on the northwest coast of Kolokolkova Bay, near the abandoned settlement of Tobseda, Malozemelskaya Tundra, northern Russia (68°35'N, 52°20'E), was studied annually between 2002 and 2006 (Van der Jeugd et al. 2003; Van der Graaf et al. 2004; Eichhorn et al. 2006; chapter 6). Body mass loss was studied during 2003-2005 in this population.

In the Baltic (BAL), birds breeding in the oldest and largest breeding colony situated at Laus holmar (57°17'N; 18°45'E) off the east coast of the island of Gotland, Sweden have been studied from 1984 to 2006 (Larsson et al. 1988; Larsson and Forslund 1994; Larsson et al. 1998; Van der Graaf 2006). Body mass loss was studied in 2000, 2003 and 2004 in this population. In the Netherlands (NL), barnacle geese were studied at Hellegatsplaten (51°42'N, 4°20'E), one of the largest colonies in the Delta area in the southwest of the country (see chapter 6), between 2004 and 2006. This colony consists of several breeding sites, mostly situated on islands. The total number of nests varied between 518 and 537 during the three study years. Body mass loss was studied in 2004 and 2005. Scientific names of species are listed in Table 7.4 or given in the text.

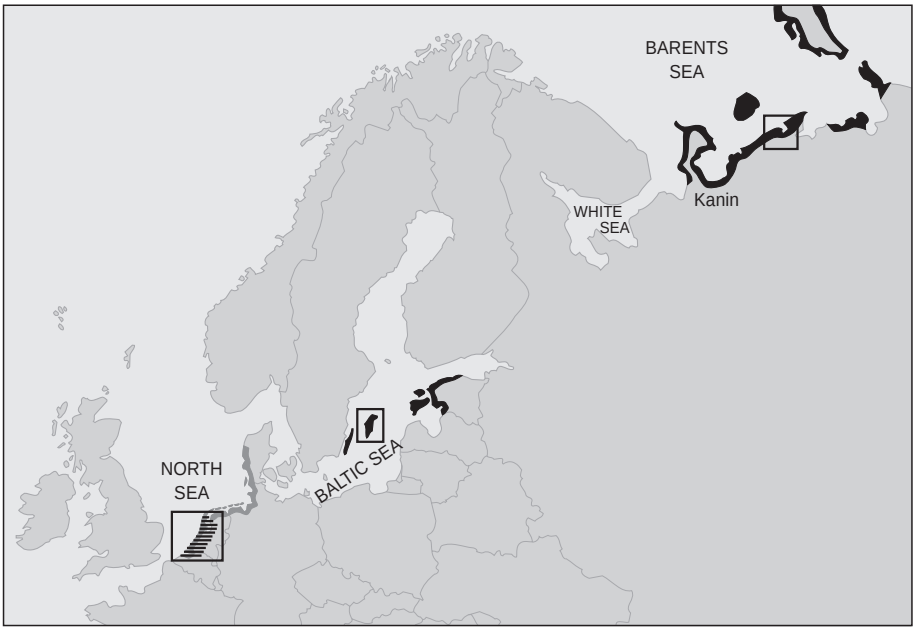

Figure 7.1. Map showing the breeding (in black) and wintering (dark grey) distribution of barnacle geese from the North Sea - Baltic - Barents Sea metapopulation and the location of the three study areas.

Measurements of body mass and reproductive parameters

Body mass of incubating females was measured by inserting a weighing machine (manufactured by T.E.L.L., Germany, type DE6K2) with a platform of 31x31 cm under the nest. This was done by completely removing a turf measuring c. 45 by 45 cm and 10–15 cm deep containing the nest, and placing the scale in the resulting hole. The nest was then carefully put on top of the scale that was fitted with an artificial nestcup (either styrene or wood) glued onto the platform. The remaining part of the scale was then covered by vegetation and soil, taking care that no material would fall into the space between the fixed and moving parts and thereby ensuring that the weight could be recorded accurately. A digital display (linked to the scale by a flexible cable) was placed on a metal standard ca 1 m high at about 5 m from the nest. The display could be read by a telescope from a distance up to ca 200 m. The observer would then retreat to an observation hide or sit concealed on the ground waiting for the female to return to the nest. When females did not return to the nest within one hour the scale was removed and another female was selected. When the female was on the nest the weight of the nest including the female was read from the display. The weight of the nest without the female was recorded

immediately afterwards when the female left the nest of her own accord or when the scale was collected. We attempted to weigh each individual at least twice, during the start and the end of the incubation period. Some females were weighted three times. In addition to using scales, some weights were obtained by trapping females on the nest using a remote-controlled clap net. In the Baltic in 2000 and 2003, all weights were gathered in this way and all females were only weighed once. All birds carried individually recognizable rings fitted to them previously or during nest captures. Body size measurements included tarsus, measured with callipers to the nearest 0.1 mm, and head, measured with a ruler at 1 mm accuracy.

For the data set used to model body mass variation during incubation clutch size was determined during repeated visits to individual nests. In most nests we marked individual eggs and could thus account for partial loss. Additional data on clutch size were taken from the literature as well as from unpublished datasets from the authors and others, including data from other study colonies from the three populations. In these data clutch size was mainly recoded in the second half of the incubation period. Egg length and egg width were measured with a dial calliper to the nearest 0.1 mm in all populations. For the Barents Sea population, additional data on egg length and width were obtained from others. Egg volume was calculated following Larsson and Forslund (1991): volume = 0.4776 x Egg length x (egg width)^2 + 6.462. Mean egg volume in a clutch was calculated as the mean of the estimated sizes of individual eggs. Because all eggs in a clutch were not always measured (e.g., due to predation), total clutch volume was calculated as mean egg volume x clutch size.

Lay date (i.e., when the first egg was laid) was backdated from incomplete clutches found during egg-laying, assuming a laying interval of 33 hrs (Alisauskas and Ankney 1992a). Incubation was assumed to start with the last egg laid for clutches up to 3 eggs, and with the pre-last egg stage for clutches larger than 3 eggs but never later than the 5-egg stage. Clutches of 7 and more eggs are more likely to include dumped eggs. We accounted for egg dumping only if this became apparent during repeated nest visits (i.e., more eggs per interval than expected or additional eggs after clutch completion). Incubation duration in barnacle goose lasts normally 24 to 26 days (Dalhaug et al. 1996; own obs.); data on body mass covered the period day 2 to 25 of incubation.

Estimation of fat and fat-free mass from isotope dilution

We employed deuterium isotope dilution (Speakman et al. 2001) to determine total body water (TBW) contents in a subsample of females from the BS (22 birds in 2003) and NL (20 birds in 2005) populations during day 2 to 21 of incubation. Birds were trapped on the nest, intra-abdominal injected with a 99.9% deuterium isotope solution (Sigma Chemicals) using 1.0 ml insulin syringes, and sampled for blood 90 min later. Birds were kept in cages with no access to food and drinking water during the isotope dilution measurements. Blood was collected from the brachial vein and stored in flame sealed micro-capillaries. An equilibrium time of 90 min was found sufficient to allow for adequate mixing of the marker solution with

the body water pool in the barnacle goose (Eichhorn and Visser 2008). In the field we administered always a dose of 1.0 ml. In the laboratory, having access to an analytical balance (Mettler AG204) and using the same type of syringes, we estimated the average dose mass of 1.0 ml at 1.1153 ± 0.0021 SD g (n=20). To estimate deuterium background levels, blood samples prior to isotope administration were taken from 5 and 4 females from the BS and NL sample, and the respective averages were applied to birds from each study site.

Determinations of δ^2H in blood samples were performed at the Center for Isotope Research, Groningen, see Eichhorn and Visser (2008) for details. In brief, blood samples were prepared by microdistillation in a vacuum line, first heating the broken tubes and then cryogenically trapping the emerging water vapor with liquid nitrogen. Water samples were stored and then automatically injected into a Hekatech High Temperature Pyrolysis unit (Gehre et al. 2004), in which the injected water was reacted with glassy carbon. The resultant H_2 and CO gases, emerging into a continuous He flow through the system, were then led through a GC column to separate the two gases in time and finally fed into a GVI Isoprime Isotope Ratio Mass Spectrometer for the analysis of δ^2H. At least three internal water standards chosen to cover the entire enrichment range of the blood samples were prepared and analysed following the same methods. All sample analyses were run at least in duplicate, more times if values differed by more than 2.5%, and we used the average of values differing from each other by less than 2.5%.

The hydrogen dilution space (TBWd) was calculated by taking into account the quantity of the dose (Q_d, mol), the ^2H concentration of the dose (C_d, atom %), the ^2H background concentration (C_b, atom %), and the ^2H concentration of individual blood samples (C_i, atom %) using following equation: $TBWd = 18.02 \cdot Q_d \cdot (C_d\text{-}C_i) / (C_i\text{-}C_b)$.

TBWd systematically overestimates TBW (by 7.1% in the barnacle goose) and we predicted the latter using the relationship $TBW = 96.034 + 0.852 \cdot TBWd$ ($r^2 = 0.976$, $P < 0.001$), established by Eichhorn and Visser (2008) for the same species. Assuming a water content in the fat-free mass of waterfowl of 66.6% (Eichhorn and Visser 2008), the fat-free mass (FFM) was calculated as: FFM = TBW / 0.666 and fat mass (FM) was subsequently inferred from body mass (BM) as: FM = BM–FFM.

Calculation of energy equivalents

We assumed that the loss of FFM during incubation consisted almost entirely of loss of protein and water, and that the potential loss of other constituents (carbohydrates and minerals) was negligible. We thus equate the loss of dry FFM to protein loss (Groscolas et al. 1991). Physiological energy equivalents of fat and protein were taken at 39.3 kJ g^{-1} and 17.8 kJ g^{-1}, respectively (Schmidt-Nielsen 1997). The energy equivalent for fat tissue was not corrected for water content (as this component is stored nearly free of water) but estimated at 4.5 g^{-1} for wet protein based on an average water content of 75% in the fat-free components of flight, leg and gizzard muscles (Box B).

Estimating daily energy expenditure (DEE)

Resting metabolic rate (RMR, at night, post-absorptive) was determined from oxygen consumption rates in five barnacle geese by Nolet et al. (1992) and in four birds by Stahl et al. (2001) using energy equivalents of 19.7 and 20.1 J ml O_2^{-1}, respectively. Combining data from both studies we detected neither an effect of study nor BM (ranging 1650-2876 g) on RMR. Therefore we apply the mean value of 5.59 ± 0.20 W (± SE, N=9) for further calculations here.

Over the first 22 days of incubation average daily recess time was 177 min for BS females and 80 min for NL birds (see Box C), and we used these values for the calculation of protein and energy budgets during steady incubation. For periods off the nest we assumed an energy expenditure of 1.9 RMR regardless of study population (Afton and Paulus 1992; Stahl et al. 2001). Average temperature during incubation was 12.4°C in the NL colony, and, assuming no costs for thermoregulation, we set energy expenditure while on eggs at 1.0 RMR for these birds. For arctic breeding birds, however, we should account for additive costs for thermoregulation.

Van der Graaf et al. (2001) adjusted the thermoregulation model of Cartar and Morrison (1997) for geese. The authors estimated that under average weather conditions during January to April costs of maintenance metabolism can be subdivided into 52% for basal metabolic needs and 48% for thermoregulation in resting barnacle geese in their wintering area. The average temperature over this period (4.1°C) is comparable with temperatures experienced by incubating geese in the BS colony (4.5°C). However, by choosing a sheltered microhabitat birds can notably save thermoregulation costs (Wiersma and Piersma 1994; Van der Graaf et al. 2001) and the insulated nest itself offers means to achieve such savings (Ar and Sidis 2002). Therefore, we assumed that thermoregulation costs accounted for an elevation of 30% of the maintenance metabolism. Overall, we estimated a DEE of 507 and 743 kJ for NL and BS birds, of which 0% and 28% comprised thermoregulation costs respectively. Energy expenditure while sitting on eggs thus resulted in 1.4 RMR for BS birds. This estimate is close to the 1.5 RMR applied by Afton and Paulus (1992) for geese and slightly lower than 1.7 RMR empirically estimated for seabirds (Tinbergen and Williams 2002).

Statistics

Each bird (individually marked) occurred only in one of the years covered by the data set. For birds with data for more than one season we selected the season with most measurements. If number of measurements was equal among seasons, we made a random selection. To control for differences in structural size between females, we used principal component analysis for the full data set including data from all three populations to combine measurements of tarsus and head length to a single structural size variable, the first principal component (PC1), which explained 85% of the total variance. A second PC1 was calculated for a sub-sample of this data set including measurements of FM and FFM components in BS and NL populations. This PC1 explained 83% of total variance. To account for the strong differences in absolute lay dates among arctic and temperate study populations (Table 7.2),

we computed 'standardized lay dates' as deviations from population-specific annual medians divided by the respective middle 50% range.

We used General Linear Models (GLM) with Tukey post-hoc tests (performed in SPSS 14.0) to analyse differences in clutch and egg size and to compare relevant variables among study populations (Table 7.1 and 7.2). In the analysis of clutch size, mean clutch size per colony and year, weighted for the number of clutches investigated, was used as dependent variable. Assumptions of normality and homogeneity of variances were evaluated using the Kolmogorov-Smirnov test and Levene's test, respectively (Zar 1999). We used a generalized linear mixed model procedure in MLwiN 2.0 (Rasbash et al. 2004) to account for inter-dependency between BM measurements taken on the same individuals during incubation within a given year. Variation of BM was modeled using following explanatory variables: PC1, day of incubation, study population, year, standardized lay date and clutch size (treated as continuous variable). In the subsample including data on FM and FFM each bird was measured only once, and we used ANCOVA in SPSS to test for variation of mass components depending on the explanatory variables: study population (fixed factor) and day of incubation and PC1 as covariates. Final models were derived by backward elimination of possible explanatory variables and their two-way interactions. All results are reported as mean ± 1 standard error (s.e.) and were considered to be significant at $P < 0.05$.

Table 7.1. GLM results investigating variation in clutch size, egg volume and total clutch volume between three populations of barnacle geese *Branta leucopsis*. Apart from differences between populations, mean clutch size differed significantly between years in the North Sea and Baltic populations.

	Clutch size			Egg volume			Clutch volume		
	df	F	*P*	df	F	*P*	df	F	*P*
Population	2,101	10.45	< 0.0001	2,333	3.80	< 0.05	2,333	21.63	< 0.0001
Year	22,101	1.24	0.23	3,333	1.02	0.38	3,333	2.53	0.06
Pop. x year	25,101	1.75	< 0.05	2,332	1.43	0.24	2,332	2.14	0.12
Effect of year by population									
North Sea	17,31	3.08	< 0.005						
Baltic	19,68	2.75	< 0.005						
Barents Sea	11,2	6.68	0.14						

Table 7.2. Summary table of data used to model body mass variation of barnacle goose females from three populations (BS = Barents Sea; BAL = Baltic; NL = Netherlands) during incubation. Sample sizes (n_i = measurements; n_j = individuals) for particular years are shown in the upper part of the table. Note that individual birds did not occur in more than one year in the data set. The lower part of the table gives mean ± standard error for relevant co-variables. Data were pooled for all available years and if there were multiple values per bird within season (i.e. body mass and day of incubation) they were first averaged. Last two columns refer to ANOVA results testing for population differences. Tukey post-hoc test results (for $\alpha \leq 0.05$) are denoted by superscript letters.

	BS		BAL		NL		Total	
year	n_i	n_j	n_i	n_j	n_i	n_j	n_i	n_j
2000			14	14			14	14
2003	25	25	4	4			29	29
2004	38	22	73	36	12	7	123	65
2005	27	17			40	28	67	45
Total	90	64	91	54	52	35	233	153

Parameter	mean ± s.e.	mean ± s.e.	mean ± s.e.	$F_{2,150}$	P
Body mass [g]	1581 ± 18 ^{a}	1650 ± 23 ^{a}	1728 ± 27 ^{b}	10.05	< 0.001
PC1	-0.13 ± 0.11 ^{a}	-0.32 ± 0.13 ^{a}	0.89 ± 0.13 ^{b}	21.48	< 0.001
Day of incubation	14.2 ± 0.6 ^{a}	11.5 ± 0.7 ^{b}	12.4 ± 0.9 ^{ab}	4.24	0.016
Clutch size	4.0 ± 0.1 ^{a}	4.8 ± 0.1 ^{b}	5.0 ± 0.2 ^{b}	12.50	< 0.001
Lay date [April]	72.5 ± 0.6 ^{a}	26.3 ± 0.6 ^{b}	23.3 ± 0.9 ^{c}	1780	< 0.001
Standard. lay date	0.21 ± 0.14 ^{a}	-0.24 ± 0.09 ^{b}	0.03 ± 0.10 ^{ab}	3.76	0.026

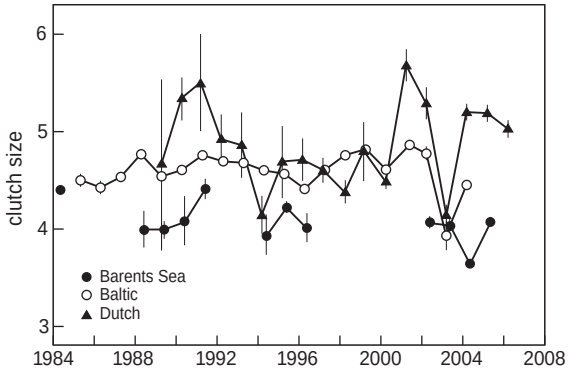

Figure 7.2. Variation in clutch size between the Barents Sea, Baltic and Dutch populations. Each point represents the weighted mean clutch size for that particular year. Data from this study, with additional data for the Arctic population from the literature (Filchagov and Leonovich 1992; Ponomareva 1992; Gurtovaya 1997; Morozov 2001; Kalyakin 2001), and additional data for the Dutch population obtained from unpublished studies (A. van der Heiden, O. Klaassen, R. Kleefstra and P. Meininger pers. comm.).

Results

Clutch size, egg volume and clutch volume

There was considerable variation in clutch size between years and populations (Fig. 7.2; Table 7.1). Clutch size increased from 4.07 (±0.08) in the Barents Sea population to 4.63 (±0.06) in the Baltic, and 4.94 in the North Sea population (±0.10). Differences in mean clutch size between the three populations were highly significant (Table 7.1). In addition, annual variation in clutch size was found to covary in the North Sea and Baltic populations ($R_{pearson}$ = 0.53, n = 16, $P < 0.05$), but not in the Baltic and Russian ($R_{pearson}$ = 0.29, n = 10, P = 0.4) or North Sea and Russian populations ($R_{pearson}$ = 0.23, n = 10, P = 0.5). The subset of data containing females for which BM loss during incubation was modelled yields a similar pattern of clutch size variation over the study colonies from the three populations (Table 7.2).

In contrast to clutch size, egg volume decreased from 90.62 mm3 (±0.62) in the Barents Sea population to 88.85 mm^3 (±0.39) in the Baltic, and 88.30 mm^3 (±0.72) in the North Sea population. Although differences in egg volume between arctic and temperate populations were significant, they could not counteract the differences in clutch size, and hence total clutch volume still increased significantly from north to south, with total clutch volume being 21% and 11% larger in the North Sea and Baltic populations, respectively, compared to the Barents Sea population (Fig. 7.3; Table 7.1).

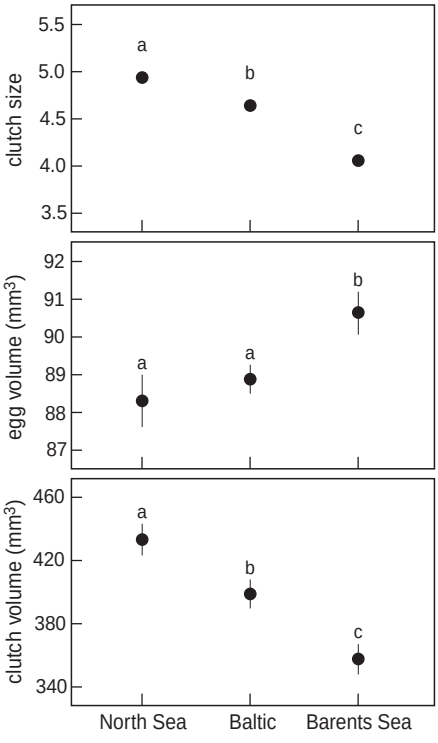

Figure 7.3. Variation in clutch size, egg volume and total clutch volume between the Barents Sea, Baltic and Dutch populations. Letters denote which populations differ significantly from each other.

Body mass

Female BM declined with incubation day (approximately linear) in all three study populations (Fig. 7.4). However, birds from the different populations differed in morphological size (PC1, Table 7.2) and PC1 explained a significant part of the variation in BM. Having accounted for these size dependent differences in BM, the model revealed significant differences in the initial BM and in the daily rate of BM loss during incubation for arctic and temperate females (Table 7.3). Average daily mass loss was almost identical in the two temperate populations in the Netherlands and on Gotland, Sweden, amounting to 17.0 and 16.5 g, respectively. BM loss observed for females incubating in the Russian Arctic was significantly lower at 10.6 g d^{-1}. Temperate breeders initiated incubation with 125 g more body stores than arctic females, which started incubation at 1742 g BM. After 25 days of incubation (the period for this species) BM converged to similar end-points among the three populations averaging 1458 g. Clutch size, (standardised) laying date and year showed no significant effect on incubation mass.

Fat and protein stores

Results of the body composition analyses from isotope dilution in a subsample of incubating females are summarized in Table 7.4 and Fig. 7.5. The pattern for BM (Fig. 7.5 A) resembles the findings from the larger data set, though population-specific differences of BM were not statistically significant in this smaller subsample. FM was significantly lower in arctic compared to temperate (NL) breeders (65 g difference on average, Table 7.4) but decreased at a similar rate of 9.4 g d^{-1} on average in females from both populations over the study period of 20 days (Fig. 7.5 B). In contrast, loss of FFM during this period differed significantly between populations (interaction Day_inc x population in Table 7.4). Temperate breeders depleted FFM at 9.3 g d^{-1}, whereas the estimated loss of 1.5 g d^{-1} for arctic breeders was not significant different from zero change of FFM ($F_{1,21} = 0.27$, $P = 0.61$; Fig. 7.5 C). Accordingly, somatic lipids accounted for 86% and 50% of female BM loss in the BS and NL population, respectively. Thus, compared to their arctic conspecifics, temperate birds started incubation with higher levels of both fat and protein stores, and retained more fat, but less protein, towards the end of incubation (note that in this data set no values were obtained beyond day 21).

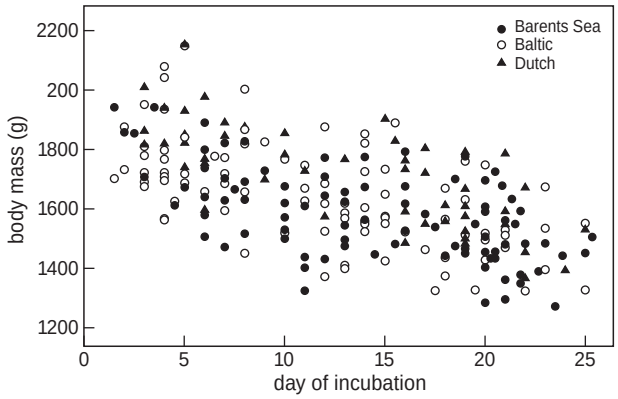

Figure 7.4. Body mass of incubating female barnacle geese. Shown are all 233 individual measurements taken on 153 birds from 3 populations.

Table 7.3. Model summary of body mass loss during incubation (day 2 to 25) of female barnacle geese from three populations (BS = Barents Sea; BAL = Baltic; NL = Netherlands). Parameter estimates are given relative to the BS population. Post-hoc comparisons among populations refer to Wald tests.

Final model		B	s.e.(B)	Df	X^2	*P*
Intercept		1742	19.9	1		
PC1		81.2	9.7	1	69.7	<0.001
Day_inc		-10.6	1.0	1	104.8	<0.001
Population	BAL	124.4	26.7	2	25.9	<0.001
	NL	125.1	32.5			
Day_inc x population	Day_inc x BAL	-5.9	1.4	2	23.2	<0.001
	Day_inc x NL	-6.4	1.6			
rejected terms						
Year				3	1.15	0.77
Standardised Lay date				1	0.61	0.43
Clutch size				1	0.46	0.50
Post-hoc comparisons of populations						
Population	NL - BAL			1	0.00	1.00
	NL - BS			1	14.80	<0.001
	BAL - BS			1	21.75	<0.001
Day_inc x population	NL - BAL			1	0.12	0.73
	NL - BS			1	15.87	<0.001
	BAL - BS			1	18.37	<0.001

Table 7.4. ANCOVA results of body mass (A), fat mass (B) and fat-free body mass (C) of incubating female barnacle geese. Mass loss during incubation (with day of incubation and PC1 as covariates) was compared for birds from the NL population (n=20) against birds from the BS population (reference category; n=22). Non-significant terms were removed by backward deletion from the model and are in brackets; given is the F-value when included in the final model. Not shown are the parameters clutch size and standardised lay date, which had no significant effect on any of the mass components.

A) Body mass					
Parameter	B	s.e.(B)	df	F	*P*
Intercept	1852	31.3	1	3494	<0.001
PC1	87.0	15.3	1	32.48	<0.001
Day_inc	-14.8	2.3	1	42.62	<0.001
(Population)			1	1.43	0.24
(Day_inc x population)			1	1.55	0.22
Final model (R^2= 0.64)			2	34.25	<0.001
Total			41		
B) Fat mass					
Parameter	B	s.e.(B)	df	F	*P*
Intercept	291.8	18.7	1	352.90	<0.001
(PC1)			1	0.19	0.66
Day_inc	-9.4	1.2	1	57.00	<0.001
Population	65.0	16.6	1	15.33	<0.001
(Day_inc x population)			1	0.40	0.53
Final model (R^2= 0.64)			2	34.84	<0.001
Total			41		
C) Fat-free mass					
Parameter	B	s.e.(B)	df	F	*P*
Intercept	1505	33.3	1	4503	<0.001
PC1	73.6	13.2	1	30.96	<0.001
Day_inc	-1.5	2.3	1	10.77	0.002
Population [a]	48.8	50.9	1	0.92	0.34
Day_inc x population	-7.8	3.4	1	5.29	0.027
Final model (R^2= 0.59)			4	13.30	<0.001
Total			41		

[a] This parameter was retained in the final model (though its main effect was not significant) because of the significant interaction with Day_inc.

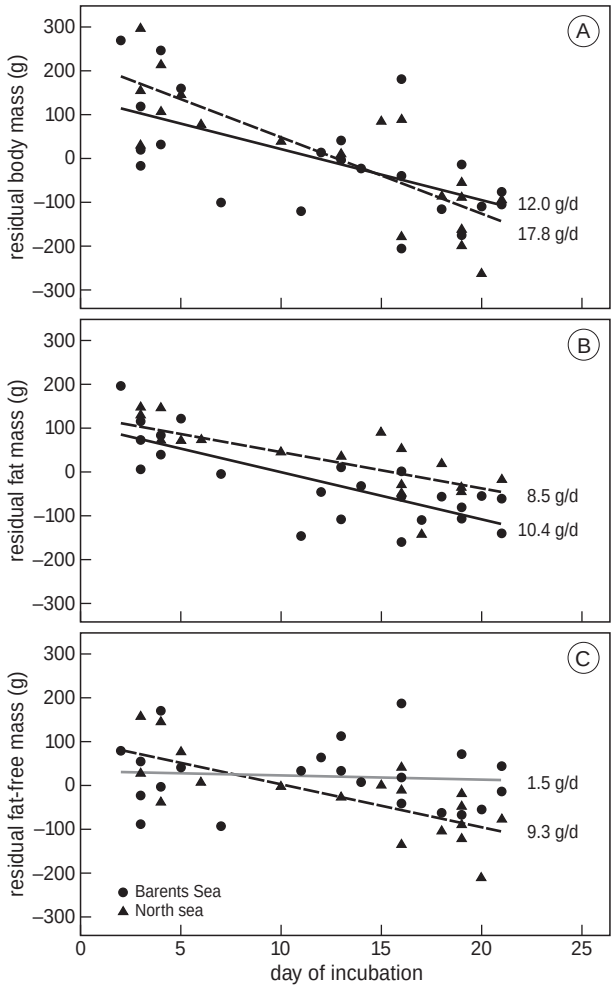

Figure 7.5. Loss of body mass (A), fat mass (B) and fat-free body mass (C) during incubation compared for birds from BS (solid line) and NL (broken line) breeding populations. Mass values represent residuals from a linear regression of mass against PC1. Values shown at the right refer to the estimated slopes of the regression lines, which were significant different from zero ($P < 0.05$) for all regressions (tested separately for BS and NL birds) except for residual FFM of BS birds (solid grey line).

Discussion

Clutch and egg size

Temperate-breeding birds laid larger clutches compared to arctic-breeding ones, although eggs were of slightly smaller size. In contrast to the pattern observed for most altricial species (Ricklefs 1980), barnacle geese thereby conform to a pattern that has also been found in other waterfowl, including northern-latitude geese (Rohwer 1992; Figuerola and Green 2006). Both somatic nutrient stores and local feeding conditions contribute to the amount of resources potentially available to the laying female and have been suggested as primary proximate determinants of clutch size (Lack 1968; Rohwer 1992; Johnson et al. 1992). Comparison of post- and pre-laying mass of females from both populations in order to infer relative endogenous and exogenous inputs to egg production is revealing. The average pre-laying BM of females in the BS colony was 1970 g (n = 45, 2003 and 2004 pooled, Eichhorn 2005). No direct measure of pre-laying BM is available for temperate breeding geese. However, if we assume similar BM gain rates for Dutch pre-laying geese and Dutch spring staging geese, we can use BM data collected at a staging site in the north of the Netherlands between 18 March and 20 April 2004 (n = 109) to extrapolate a BM of 1999 g for 25 April, the average laying date of NL birds. Because of the assumption that virtually all of the staging birds in this sample belonged to the BS population (based on ring-readings) and the notable differences in structural size (PC1) of BS and NL birds (Table 7.2) and its effect on BM (Table 7.3), we have to correct these pre-laying masses accordingly. When this is done, the estimated BM losses during laying are 2009-1867 = 142 g for 5 eggs (NL) and 1981–1742 = 239 g for 4 eggs (BS). Apparently, the better feeding conditions during egg-laying allow temperate-breeding birds to allocate a higher proportion of locally-obtained resources directly to egg production, whereas arctic-breeding birds have to draw more from body stores at that time of the season. Moreover, arctic nesters have to pay the cost of migration and start breeding with lower body stores compared to temperate birds.

Although of smaller body size than barnacle geese from the NL population, the arctic-breeding BS birds laid larger eggs. Resource limitation for the laying female (increasing with latitude/migratory distance) in combination with egg-size adjustment to a harsh environment (Koskimies and Lahti 1964) may enhance the inverse relationship we found between egg size and clutch size among our three study populations. A trade-off between egg size and number has been shown at the interspecific level for waterfowl, including geese, but has not been found within species of waterfowl (Christians 2000 and references therein).

Body size and body mass

If we want to derive any general conclusions about body size differences between temperate and arctic populations (Table 7.2), we have to take into account that adult body size is related to nutritional conditions during the juvenile growing phase (Larsson and Forslund 1991; Sedinger and Flint 1991). Adult body size of successive cohorts in the Baltic was found to decrease rapidly as a result of

increased competition for food when colonies grew older (Larsson et al. 1998). The Baltic population is currently decreasing in terms of breeding pairs, and the main study colony was over 30 years old when the data we present here were collected. We therefore attribute the small body size of Baltic birds to this competition (or density) effect. However, the BS, and especially NL, populations still enjoy rapid growth, indicating better food conditions for offspring growth in these populations. The difference in body size between these populations might tentatively hint at temperate populations evolving towards a larger body size.

We found marked differences in the rate of BM loss during incubation between arctic- and temperate-breeding barnacle geese, with temperate-breeding females losing up to 60% more mass each day. However, temperate-breeding females initiated incubation with a body mass that was 125 g higher than that of arctic-breeding females. Assuming the rates we found to be constant over the whole incubation period, female BM loss until end of incubation (day 25) amounted to 15% (BS), 22% (BAL) and 23% (NL) of BM at start of incubation. These values are conservative estimates, because few measurements are available for the first and last two days of incubation (see Fig. 7.4) when the rate of mass loss may have been even higher due to changing lipid and protein catabolism, a phenomenon which has been observed in fasting geese (Le Maho et al. 1981; Boismenu et al. 1992).

BM (after laying) was not related to clutch size or (standardised) lay date. Because clutch size decreased with (standardized) laying date ($F_{1,149} = 4.98$, $P = 0.027$, accounting for population effects in the model), BM at pre-laying most likely decreased with laying date. A parallel decline of both pre-laying BM and clutch size would then cause a similar BM after laying. Bêty et al. (2003) showed how greater snow geese might optimise individual egg-laying decisions (when and how many) according to their body condition. That females (of the same population) deplete their body stores during laying to similar levels at clutch completion regardless of clutch size has been observed, for instance, in lesser snow geese, and is clearly adaptive for birds which draw mainly on body stores during incubation (Ankney and MacInnes 1978). Our results indicate that the actual level of a post-laying nutrient reserve threshold was similar among either temperate or arctic-breeding females but was different between populations: temperate breeding geese laid one egg more; nevertheless, they commenced incubation with larger nutrient reserves than geese from the arctic population.

Depletion of protein and energy stores during steady incubation

Almost the entire loss of BM through incubation (day 2 to 21) in arctic-breeding females comprised fat, whereas in temperate females both fat and lean mass contributed equally to the decrease of BM. Energy density of wet lean tissue is considerably lower than that of fat (see methods). The energy contents of 1 g utilised BM were 21.1 kJ in NL birds and 34.9 kJ in BS birds (calculated from the slopes in Fig. 7.5). Consequently, and despite the strong difference in BM loss, energetic yields from body stores differed less between populations, amounting to 376 and 415 kJ d^{-1} in NL and BS birds, respectively.

To look for proximate reasons to explain the differential use of body components in the two study populations we have to consider the budget of nutrient and energy expenditure and uptake. Both lipid and protein depletion depend on energy expenditure. However, the ability to spare proteins during periods of fasting additionally depends on the organism's adiposity (Caloin 2004). Given the consistently higher lipid reserves (and lower energetic costs, see below) in temperate-breeding females, their higher use of somatic protein cannot be caused by energetic demands. Instead, we suggest that the reduced (feeding) recess time of NL birds was insufficient to replace much of their endogenous protein loss. Over the first 22 days of incubation average daily recess time was 177 min for BS females but only 80 min for females from the NL colony (see Box C).

Daily maintenance nitrogen requirements of 0.44 and 0.45 g kg^{-1} have been reported for magpie goose *Anseranas semipalmata* and Cape Barren goose *Cereopsis novaehollandiae* (Dawson et al. 2000; Allen and Hume 2001). Le Maho (1981) measured a daily total endogenous N loss of 0.16 g kg^{-1} in domestic geese during starvation (at start of phase two). Using the average value of these three studies as proxy for barnacle geese of 1660 g BM at mid incubation yields maintenance protein requirements of 3.6 g d^{-1} (assuming a nitrogen fraction in protein of 0.16, Blaxter 1989). This would mean that NL birds, which experienced a net loss of 2.3 g d^{-1} of dry somatic protein (at 75% protein hydration, see methods) could only balance 35% of these requirements during their recess bouts, whereas BS birds apparently gained 90% of their requirements during feeding recesses. Translating the protein input from feeding into nitrogen retention per daily recess time reveals 2.6 (NL) and 2.9 (BS) mg min^{-1}. These values are comparable to the 2-4 mg min^{-1} N retention rates in barnacle and dark-bellied brent geese estimated during the period of intensive protein deposition in spring (Prop and Black 1998; Prop and Spaans 2004). Assuming that BS and NL birds retained similar proportions of ingested N, the similar N retention rates indicate comparable feeding conditions in both breeding habitats. This is consistent with equally high N contents in forage plants collected at both sites (see chapter 6).

Unlike endogenous nitrogen losses, energy expenditure should certainly be lower in temperate-breeding birds, since ambient temperatures were almost always above the lower critical value at which costs for thermoregulation will be induced (Box C). In line with these considerations, daily energy expenditure (DEE) measured during incubation by the DLW technique was about 50% higher in eight species of arctic breeding shorebirds compared to similar sized temperate-breeding birds (Piersma et al. 2003). Also, the higher nest attentiveness of geese from the NL population (Table 7.4) minimized costs for activities (mainly feeding) off the nest. Of the estimated DEE of 507 and 743 kJ (see methods for details) NL and BS birds, respectively, would have balanced 74 and 56% with their body stores. Balancing the remaining costs through feeding would demand an intake rate of 1.6 (NL) and 1.9 kJ (BS) per min off the nest, which seems feasible if compared to average rates of 1.5 to 2.4 kJ min^{-1} found for barnacle geese foraging in different habitats during spring (Prop and Black 1998).

Preliminary energy budgets for the entire incubation period

Assuming the daily rates of depletion of FFM and FM that have been determined for the period day 2 through 21 (Table 7.4, Fig. 7.5) to apply throughout the 25 day incubation period the body stores present at the start and again at hatch can be estimated (see also appendix). For the arctic birds 260 g of the original FM of 292 g would be depleted during incubation, leaving a residue of 32 g at hatch. These figures corroborate the provisional fat budget for Russian birds presented by Drent et al. (2007), where the FM at commencement of incubation was estimated at 310 g (and residue at hatch hence slightly higher than in the present exercise). The FFM of arctic birds declined by only 38 g (of the 1505 g available at commencing incubation 1467 g would remain at hatch). For the non-migratory temperate counterparts (NL) the corresponding estimates are 213 g for FM depletion (body stores declining from 357 g at start to 144 g at hatch) and a loss of 233 g for FFM (1554 g at start, 1321 g at hatch). BM at hatch would converge at 1499 g for arctic birds and 1465 g for temperate breeders, but as noted the composition of the body differs. Although these figures require confirmation by sampling females at hatch, the preliminary calculations support the notion that females in the arctic work to a stringent budget and must supplement their endogenous energy source by feeding throughout incubation to avoid complete depletion of their FM. In this view the time off the nest is adjusted to assure the exogenous energy input needed to balance the budget (see calculations above). Since the temperate breeders commence incubation with higher FM and moreover face lower daily costs they can reduce their daily feeding time compared to their arctic counterparts. Table 7.5 shows that attentiveness during incubation (% time on nest) is consistently higher in barnacle geese incubating in temperate regions (two studies) compared to the arctic birds (two studies) by a margin of 5%. It will be seen from the table that species breeding in the arctic generally achieve incubation attentiveness in the range 88-99.5%. There are only a few previous estimates of the contribution of endogenous stores to total incubation cost and these do not reveal a simple pattern to either body mass (see Thompson and Raveling 1987) or migration distance. Relating species/population means of BM loss to nest attentiveness underlines the importance of incubation recesses for the regulation of endogenous nutrient reserves (Fig. 7.6). Two studies (on emperor and white-fronted goose) 'fall off the line' and may require confirmation.

Alsos et al. (1998) showed that individual barnacle geese females with rich food supplies in their feeding territory achieved higher attentiveness than neighbours with fewer resources, again suggesting that time off to feed is regulated to achieve a given energetic intake. Prop et al. (1984) showed that individual barnacle geese subsequently abandoning incubation spent increasing amounts of time feeding daily, suggesting that these birds were in poor body condition and needed to compensate for this (see also Schmutz et al. 2006). Aldrich and Raveling (1983) studied incubation attentiveness in 13 pairs of captive (and wing-clipped) western Canada geese kept in large flight pens in California. Females were weighed at the onset and thereafter at weekly intervals, and incubation constancy monitored by weighing platforms. Overall attentiveness was 97.5% (and lost 27% of initial body

Table 7.5. Body mass loss and nest attentiveness of northern geese during incubation.

study/species/subspecies/population		g BM at start of incubation	% BM loss	%Time on nest	km from wintering area*	% energy stores to inc.
1) Greater Snow G.	*Anser caerulescens atlanticus*[1]	2590	17	91.4-93	4000	
2) Lesser Snow G.	*Anser c. caerulescens*	2530	32	97.1	3400	78
3) Emperor G.	*Anser canagicus*	2230	21	99.5	1500	
4) Gr. White-fronted G.	*Anser albifrons albifrons*[2]	2635	24.1	99.2	4500	
5) Western Canada G.	*Branta canadensis moffitti*	4300	27	97.5	0	
6) Dusky Canada G.	*Branta c. occidentalis*	3206	22	91.7	2600	58
7) Cackling Canada G.	*Branta c. minima*	1387	21	93.6	3300	39
Barnacle Goose	*Branta leucopsis*					
8)	Great Britain	2020	28	94.8	0	
9)	Netherlands (NL)3	1867	23	94.6	0	74
10)	Baltic (BAL)[3]	1866	22		1000	
11)	Barents Sea (BS)[3]	1742	15	89.1	3200	56
12)	Spitsbergen[4]			89.5-93.2	3000	
13) Dark-bellied Brent	*Branta bernicla bernicla*[5]	1269	16	87.6	4500	52
14) Light-bellied Brent	*B. b. hrota*	1143	11	81.7	3200	17
15) Black Brent	*B. b. nigricans*[6]			89.6		

Data from Afton and Paulus (1992), updated for [1](Reed et al. 1995; Poussart et al. 2001), [2](Spaans et al. 1999), [3](this study; nest attentiveness Box C this thesis), [4](nest attentiveness as 89.5% from Tombre and Erikstad 1996; 93.2% from Tombre et al. unpubl. data for 1997; 89.9% from Alsos et al. 1998), [5](Spaans et al. 2007), [6](Thompson and Raveling 1987). * Breeding location taken from original source; if winter sites were not given therein, taken from Owen (1980).

mass) but the individual data showed that total recess time during incubation was dependent on BM at onset, a relation also evident on a weekly basis. As expected, BM loss between weightings depended on weekly recess time (individuals with shorter feeding times accepting higher losses of body mass). These three studies on individual incubation constancy support the notion that feeding time is adjusted on the short term in relation to state of the body stores.

Factors explaining differences between arctic and temperate populations

We have shown that the composition and dynamics of nutrient reserves used to sustain females through incubation can differ remarkably among high-latitude and temperate breeding barnacle geese. While saving on travel costs and profiting from a relatively higher input of current diet to egg production enabled temperate geese to lay larger clutches and still start incubation with larger nutrient reserves, they make less use of food uptake through incubation and deplete in particular their protein stores more than arctic geese. What may explain these different strategies of nutrient reserve use?

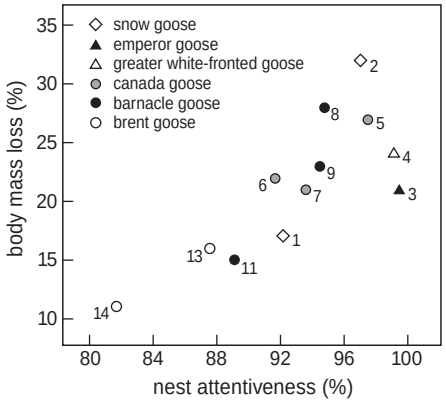

Figure 7.6. Body mass loss during incubation in relation to nest attentiveness. Species of geese are marked by common symbols. Numbers refer to studies presented in Table 7.5.

Barnacle geese from all three populations usually undergo moult on their breeding grounds. Even if nutrient and energy demands of moult may be largely or fully supplied by feeding, moult is unlikely a period of significant nutrient deposition (Hohman et al. 1992). Moreover, BS birds have to prepare for 3,200 km fall migration, whereas NL birds overwinter in or near to their breeding and moulting grounds. Therefore, temperate-breeding females might tolerate higher BM losses during incubation because they have a much longer period of recuperation before entering the moult. The interval between hatching (when nutrient reserves are depleted at its most) and start of moult is ca 35 days in BAL and NL, but only 16 days long in BS (chapter 6). According to this interpretation, arctic-breeding females regulate their daily deposition rate of protein to avoid depletion of their body stores. Arctic birds thus accept longer daily feeding times (Table 7.5). Further work will be needed to quantify other factors in the nest attendance trade-off (including predation risk, protection from egg-dumping, etc.). For a better understanding, we also need to extend our knowledge of body composition to embrace the post-incubation period.

Acknowledgements

We want to thank J. Anisimov, D. Ochinashko, M. Schouten, A. Pouw, J. van Dijk for their help in the field. B. Verstappen-Dumoulin determined the ^{2}H enrichments. K. Litvin and M. van Eerden played an important role in the organization and support of the Dutch-Russian expeditions to Tobseda. Further support by the Institute of Biology in Syktyvkar, by the administrations of the Nenets Autonomous District and the State Nature reserve Nenetskiy, and by the Russian Hunters Association is gratefully acknowledged. The study at Hellegatsplaten, the Netherlands, was possible due to support of the owner, Staatsbosbeheer.

Financial assistance came from the Dutch Institute for Inland Water Management and Waste Water Treatment (RIZA), the Schure-Beijerink-Popping Fonds (KNAW-Royal Dutch Academy for Science) and the Nicolaas Mulerius Fonds of the University of Groningen. GE was supported by travel grants from the European Science Foundation (BIRD programme) and scholarships from the 'Marianne und Dr. Fritz Walter-Fischer Stiftung', Germany, and the 'Ubbo Emmius Programme' at the University of Groningen.

Appendix 7.1. Incubation fact sheet for barnacle geese from the Barents Sea (BS) and the Netherlands (NL).

	BS	NL	remark
Before incubation:			
Estimated pre-laying BM (g)	1981	2009	Eichhorn (2005) and extrapolated
BM at start of incubation (g)	1742	1867	full data set on BM
Clutch size	4.07	4.94	
Egg volume (mm^3)	90.62	88.30	
Clutch volume (mm^3)	357.2	432.1	
During incubation:			
Incubation duration (d)	25 (22-26)	25 (22-26)	(Dalhaug et al. 1996; own obs.)
Time off nest per day (min)	177	80	first 22 days of incubation
Daily mass loss BM (g)	10.6	17	full data set on BM
Daily mass loss BM (g)	12	17.8	subsample for body composition
Daily mass loss FM (g)	10.4	8.5	subsample for body composition
Daily mass loss FFM (g)	1.5	9.3	subsample for body composition
Energy budget			
RMR (kJ/d)	483	483	for BM at half way incubation
DEE in RMR units	1.7	1.05	
Estimated DEE (kJ/d)	743	507	
Energy from body (kJ/d)	415	376	
Shortfall (kJ/d)	328	131	
Net intake needed (kJ/min)	1.85	1.64	
Contribution body (%)	56	74	
FM dynamics			
at day 0 (g)	292	357	
Depletion over 25 d (g)	260	213	
at hatch (g)	32	144.5	Day 25 of incubation
FFM dynamics			
at day 0 (g)	1505	1554	
Depletion over 25 d (g)	38	233	
at hatch (g)	1467	1321	Day 25 of incubation
FFM + FM at hatch (g)	1499	1465	Day 25 of incubation

Box D

Deposition of body stores in pastureland and salt marsh

Götz Eichhorn

Barnacle geese, like many other waterfowl, have increasingly utilised improved grassland during the past 20 years, where forage quality is enhanced due to intensive agricultural fertilization (Van Eerden et al. 2005). It has been argued recently that geese feeding on agricultural pastures benefit from a higher rate of fat deposition, however, at the costs of protein accretion (Prop and Black 1998; Prop and Spaans 2004). However, evidence is inconsistent concerning the questions whether pastureland may represent a second choice habitat (Ebbinge 1992) for arctic geese and whether its usage as foraging site may impair the deposition of body stores and subsequent reproductive success (Prop and Black 1998; Spaans and Postma 2001). Here I investigate changes of body mass and body composition of barnacle geese on the Dutch Wadden Sea island Schiermonnikoog during spring staging period. I compare birds staging in an unmanaged natural salt marsh in the eastern part of the island with birds using heavily fertilised agricultural pastures six kilometres west of it (for a description of the study site see Van der Jeugd et al. 2001; Bos and Stahl 2003).

Methods

The total data set in the present analysis consists of BM measurements on 234 birds of both sexes and two age classes including immature birds (in their second calendar year, determined by presence of juvenile feathers: 11 females, 8 males) and adult birds (i.e., older than 1 year: 109 females, 106 males). By means of isotope dilution (ch. 2, 7) I estimated fat-free mass (FFM) and fat mass (FM) in a subsample of 54 adult females. Birds were sampled (caught, measured and released) at five occasions during the period 18 march to 20 April 2004 from agricultural pastures (three occasions) and salt marshes (two occasions). Further measurements included length of tarsus, head and wing. I use first principal component scores (PC1) generated from a principal component analysis (PCA) of these three structural measurements in order to account for variation in body size.

Results

Table Box D.1 (A) shows results of an analysis on BM comprising all birds in the data set, which are further illustrated in Fig. Box D.1. If corrected for structural size (i.e., including PC1 in the model) females and males did not differ in body mass. A quadratic date effect indicates a levelling off in BM gain towards the end of the study period. Immature birds were 83 g lighter than adults if both sexes are combined and 106 g lighter if only females are concerned (Table Box D.1B). Both sexes combined, pasture birds were on average 73 g lighter than salt-marsh birds. This can be mainly attributed to the condition of males. When females were tested separately no difference in BM between habitats was detected and BM increased linearly with date at a rate 10.3 g d^{-1} throughout the study period (Table Box D.1B), whereas habitat and quadratic date effects remained significant when males alone were tested (model not shown). The rate of BM gain did not differ between habitats regardless if sexes combined or separately are concerned.

FFM of adult females (corrected for differences in structural size) was the same in both habitats and increased with 3.6 g d^{-1} (Table Box D.1C), which should reflect the gain of wet protein mass. For the same sample BM increased at 10.9 g d^{-1} and the difference of 7.3 g d^{-1} is considered to reflect the gain of FM (Fig. Box D.2). Thus FM and wet protein mass contributed with 67% and 33%, respectively, to the BM gain observed during the study period. This translates into a ratio of fat to dry protein of 8.1, assuming a 75% water content in the gained fat-free component (assumed to be mainly muscle tissue; Box B). An analysis of fat-free mass changes over time following the approach suggested by (Lindström and Piersma 1993) assumes a closed population wherein body mass deposition is synchronised among

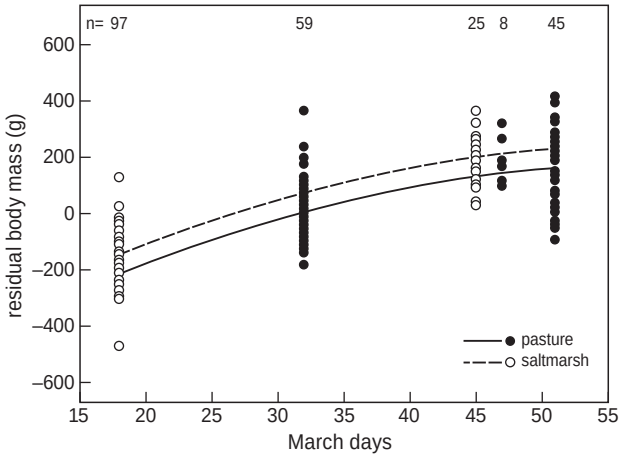

Figure Box D.1. Body mass development of barnacle geese staging in agricultural pastures or salt marsh habitat on the Dutch island Schiermonnikoog. Plotted is the residual body mass (corrected for body size) of both sexes and adult and second calendar year birds combined. See Table Box D.1 for details on the statistical model. Sample sizes are given in the top of the figure.

Table Box D.1. ANCOVA results of body mass for all birds (A), body mass of females only (B) and fat-free body mass of adult females (C) of barnacle geese caught during spring staging on the Dutch island of Schiermonnikoog. PC1 refers to the first principal component from a PCA of tarsus, head and wing. When both sexes were included in the model (as in A) we used PC1 scores from a single PCA over all birds. When only females were concerned (B and C) we used PC1 scores generated for females only. Main effects and all possible two-way interactions were tested and non-significant terms were removed by backward deletion from the models. Some non-significant terms (n.s.) are shown in brackets; given is the F-value when included in the final model. Estimated coefficients (b) with associated standard errors (s.e.) are given only for statistical significant parameters. Note that the "Date" variable refers to March days with the intercept set at March day=0. Coefficients for "Habitat" and "Age" are set relative to reference category "salt marsh" and "adult", respectively.

A) Body mass					
Parameter	B	s.e.(B)	df	F	*P*
Intercept	1236	68.8	1	237.93	<0.0005
PC1	109.2	6.7	1	267.14	<0.0005
Date	27.8	4.8	1	34.01	<0.0005
Date^2	-0.2	0.1	1	12.62	<0.0005
Age	-82.5	24.2	1	11.64	0.001
Habitat	-72.6	19.9	1	13.34	<0.0005
(Sex)			1	0.57	n.s.
(Date x Habitat)			1	0.98	n.s.
Final model (R^2= 0.77)			5	152.75	<0.0005
Total			233		
B) Body mass females					
Parameter	B	s.e.(B)	df	F	*P*
Intercept	1403	25.05	1	2280.16	<0.0005
PC1	70.4	9.8	1	51.77	<0.0005
Date	10.3	0.7	1	197.50	<0.0005
(Date^2)			1	0.20	n.s.
Age	-106.3	33.7	1	9.98	0.002
(Habitat)			1	1.70	n.s.
(Date x Habitat)			1	1.37	n.s.
Final model (R^2= 0.72)			3	97.01	<0.0005
Total			119		
C) Fat-free mass adult females					
Parameter	B	s.e.(B)	df	F	*P*
Intercept	1342	30.1	1	1983.71	<0.0005
PC1	62.1	10.9	1	32.15	<0.0005
Date	3.6	0.8	1	21.13	<0.0005
(Date^2)			1	1.87	n.s.
(Habitat)			1	0.02	n.s.
(Date x Habitat)			1	1.54	n.s.
Final model (R^2= 0.56)			2	31.93	<0.0005
Total			53		

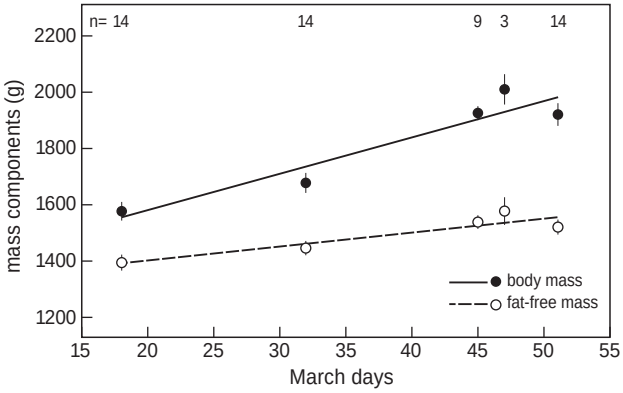

Figure Box D.2. Development of body mass components in adult female barnacle geese during spring staging on the Dutch island Schiermonnikoog. Changes in total body mass (BM) or fat-free mass (FFM) did not differ between geese from agricultural pastures or salt-marsh habitat. Rates of mass increase are 3.6 g d^{-1} for FFM and 10.9 g d^{-1} for BM (10.3 g d^{-1} if BM for all females in the data set is modelled, see Table Box D.1 B and C for statistical models and tests). Sample sizes are given in the top of the figure.

individuals. We know that barnacle geese on Schiermonnikoog belong to populations breeding in Arctic Russia and in the Baltic. The proportion of Baltic birds in the sample likely decreased towards the end of the study period (20 April). Also, it cannot be excluded that birds from these populations differ in their stage of deposition at a given time point or aim for a different composition of stores in general. Van der Meer and Piersma (1994) suggested alternative approaches for an estimate of the composition of body stores, which may account better for individual variation in stage of body store deposition at a given sampling event. I applied their model 2b and regressed FFM corrected for structural size on FM (FM was not related to PC1). This yields a slope of 0.235 indicating a contribution of wet protein to total BM gain of 23.5% (see Fig. Box D.3) and a fat/dry protein ratio of 13.0.

Discussion

I conclude that wet protein comprised a quarter to a third of body stores deposited by adult females during spring staging in the Wadden Sea. Total gain rates and composition of stores appeared to be similar for birds staging in agricultural pastures and salt marshes. Immature birds showed lighter BM than adults, but a difference in BM gain rates between age groups could not be detected. McLandress and Raveling (1981) found similar age effects in giant Canada geese *Branta canadensis maxima* before initiating spring migration in April. Their argument that immature birds may be not in preparation for reproduction as Canada geese almost never nest at this young age seems applicable also for the barnacle goose (Black et al. 2007). It would be of course interesting to know what precisely are the proximate factors preventing them from doing so (e.g., experience, dominance, physiological development).

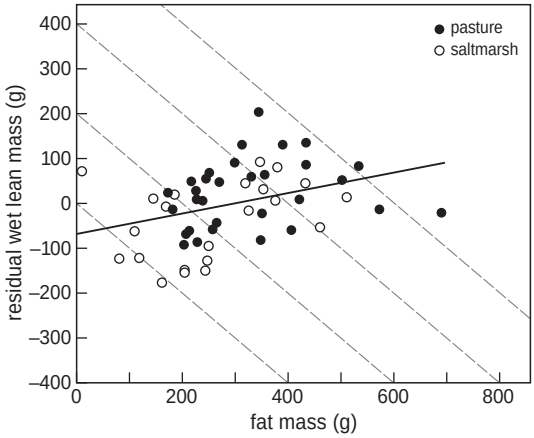

Figure Box D.3. Residual fat-free mass (accounting for PC1) against fat mass of adult female barnacle geese from the Dutch island Schiermonnikoog in spring (same data as in Table Box D.1C and Fig. Box D.2). The slope (y = 0.235x; $F_{1,53}$ = 7.35, P = 0.009) did not differ between geese from different habitats ($F_{1,53}$ = 2.80, n.s.) depicted by closed circles (pasture) and open circles (saltmarsh). Diagonal dashed lines are lines of equal body mass.

Adult female giant Canada geese from the same study sampled on 4-7 March and on 4-6 April revealed a ratio of fat to dry protein in the gained body stores of 9.5, which is within the range of estimates for barnacle geese in the Wadden Sea. The composition of stores can be highly variable among goose species and can vary considerably even within species (see Table 8 in Prop and Black 1998). For barnacle geese from the Spitsbergen population staging in northern Norway Prop and Black (1998) recorded fat/protein ratios of stores of 1.2 to 1.4 while using traditional saltmarsh sites but measured a fat/protein ratio of stores of 22.6 for geese using nearby agricultural pastures. Similarly, composition of gained stores may vary during periods of deposition. For instance, comparing body composition of the female giant Canada geese from 4-7 March to an earlier sample taken 12-16 February yields an increase of total BM and FFM but a decrease of fat mass (McLandress and Raveling 1981). Such temporal variation in composition of stores with fat/protein ratios often increasing during pre-migratory deposition has been observed also in several other studies (Alisauskas and Ankney 1992a; Gauthier et al. 1992; but see Sedinger et al. 1992; Battley and Piersma 1997; Prop and Spaans 2004) and may be well controlled by endogenous circannual programs (Dietz et al. 1999).

Acknowledgements

I want to thank all who assisted in the fieldwork and Kees Oosterbeek in particular, who provided tools and invaluable skills to make the capture of geese possible. Analysis of the ^{2}H enrichments was provided by Harro Meijer and Berthe Verstappen-Dumoulin at the CIO of the University of Groningen.

Chapter 8

General discussion

Götz Eichhorn

Flexibility and constraints of migration and breeding in the barnacle goose

This thesis deals with issues of time and energy management and costs and benefits of migration. Behavioural decisions on migration and reproduction will directly mould the pattern of energy acquisition and use. On the other hand, behavioural choices are limited by the access to energy and nutrient sources. Our studies have revealed a remarkable flexibility in timing of migration as well as reproduction in the barnacle goose. Starting off from the same wintering area geese of the sedentary North Sea population hatch their young at a time when arctic-breeding conspecifics have not even reached their breeding sites (ch. 3, 6). Birds from the same arctic breeding colony may leave the wintering area as long as eight weeks apart, and even the very same individual may decide to depart from there 45 days later than it did the year before (ch. 4). Throughout, I have tried to assemble appropriate data from the past to compare with the current situation. A first point in the discussion here concerns fuelling for migration in spring.

Deposition of body stores: now and then

The function of the Baltic as traditional fuelling site on the way to arctic breeding grounds has been taken over by the Wadden Sea for an increasing part of the flyway population, and we propose a capacity problem in the Baltic as the key explanation for this (ch. 3, 4). In the chapter discussions so far it remained an intriguing possibility that not only fuelling prospects in the Baltic have deteriorated relatively to those in the Wadden Sea, but, additionally, opportunities for fuelling in the Wadden Sea may have improved over past decades. Figure 8.1 illustrates the seasonal pattern of body mass change in adult female barnacle geese caught/shot along the spring migratory route. For the Wadden Sea area recent data can be compared to data collected 15 to 25 years ago and reveals striking differences: the rate of mass gain more than doubled compared to former times, though birds nowadays show a lower body mass early in the season. Body mass reached a same level in each of the data sets by mid April (day 45). This date coincides with the traditional departure date when the geese used to move to the Baltic for further deposition of body stores, whereas nowadays a large proportion of the population continues fuelling in the Wadden Sea until mid May, apparently at a higher rate than decades ago.

According to the optimal migration model this new strategy will be favoured only if the fuelling rate in the Baltic falls below 88% of that in the Wadden Sea (ch. 4). That is, below 10 g d^{-1} nowadays, and would mean that the formerly high gain rate in the Baltic (21 g d^{-1}) has decreased by 52%. Such a scenario is corroborated by findings of Van der Graaf et al. (2006b) indicating a currently high grazing pressure in the Baltic resulting in lower food availability than at staging sites in the Wadden Sea.

Food availability is only one of the factors limiting gain rates. For instance, the advantage of longer daylight periods in the Baltic provides potentially longer foraging time to the geese, and may compensate for the lower food availability

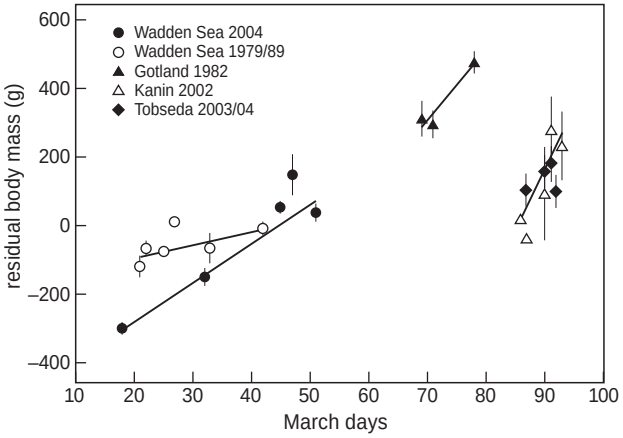

Figure 8.1. Residual body mass (from a regression of mass on wing length) of adult females at pre-migratory sites in the Wadden Sea (WS), at staging sites in the Baltic (Gotland) and White Sea (Kanin), and upon arrival in the breeding area at Tobseda. Shown are daily means ± SE. Note the different years of sampling. Regression lines are depicted for all but Tobseda data, and yield gain rates [g d^{-1}] of 11.3 for WS 2004 ($F_{1,108} = 176.8$, $P < 0.0005$); 3.8 for WS 1979/89 ($F_{1,102} = 5.53$, $P = 0.021$); 20.7 for Gotland 1982 ($F_{1,35} = 13.39$, $P = 0.001$). The estimated slope of 37.0 g d^{-1} for Kanin lacked statistical significance ($F_{1,22} = 1.47$, $P = 0.240$). Data from WS 1979/89 and Gotland 1982 were kindly provided by B.S. Ebbinge (see also Ebbinge et al. 1991).

compared to Wadden Sea sites. On the other hand, this potential benefit might be lost due to increased disturbance from white-tailed eagles. Their numbers are boosting in the Baltic over the past three decades (ch. 4) and assessing their direct and indirect effects on staging geese seems revealing.

The importance of pre-breeding staging sites for Arctic breeders

The dramatic change in migratory schedule concerns only the first part of the journey up to the Baltic. Departure from the Baltic remained stable over the past decades. Our expeditionary work coupled with tracking of individual geese has revealed the stopover sites connecting the Baltic with the breeding sites. After birds have left the Baltic they stay for a remarkably constant period (3 weeks) in arctic pre-breeding sites (notably the Dvina river delta and Kanin peninsula) before they finally arrive in the colony ca. four days prior to egg-laying (ch. 3, 5; Eichhorn 2005). The geese replenish some of the body stores lost during migration at these arctic pre-breeding sites, and females enter the phase of rapid follicular growth 12 days before egg-laying. The high estimate of daily body mass gain for Kanin lacked statistical significance, probably due to the small sample of geese collected over a very short time period of seven days (Fig. 8.1). However, preliminary results from field studies on food intake yielded similarly high gain rates of more than 30 g d^{-1} (Eichhorn, unpubl. data). High digestibility of young food plants and, in particular,

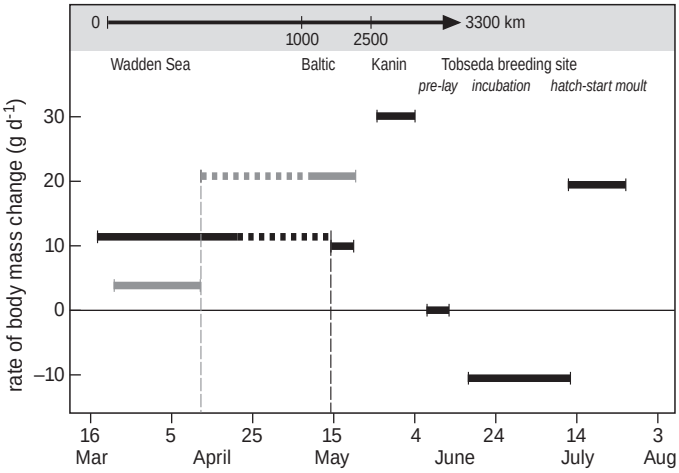

Figure 8.2. Average rates of body mass change in arctic-breeding female barnacle geese at spring staging sites and during various stages in the breeding area. Black and grey colour indicate present and former (before 1990) estimates, respectively. Vertical dashed lines mark former (left) and present (right) dates of mass departure from the Wadden Sea. Note that timing of mass departure from the Baltic occurs around 20 May and has not been changed over past decades. Solid lines refer to periods with data coverage; for the Baltic the current rate was assumed at 88% of that in the Wadden Sea (see Fig. 8.1 and text for details). Horizontal stippled lines refer to extrapolations from these data.

the long feeding days allowed for such impressive intake rates at this important staging site in the eastern White Sea. An important finding in chapter 3 was that a delay of departure from the Baltic resulted in a delay of nest initiation, supporting the proposal by Drent and Daan (1980) that late-laying individuals choose to accumulate more/ adequate reserves for reproduction at southern staging sites. Thus, females can profitably feed not far from breeding sites and are not entirely dependent on body stores for egg synthesis upon arrival at the colony where little food is available (Rohwer 1992).

In Figure 8.2 I assembled the estimated gain rates at the major spring staging sites together with rates of body mass change during various stages while in the Russian breeding area. The conclusion is that spring fuel deposition rates in the Baltic and the Wadden Sea that formerly differed markedly have recently converged by deteriorating in the Baltic and improving in the Wadden Sea. There are no tangible signs of a possible buffer effect (Kluyver and Tinbergen 1953; Gill et al. 2001; Gunnarsson et al. 2006) associated with the saturation of the Baltic sites and penalising the recently evolved alternative strategy of delayed departure from the Wadden Sea. Timing of egg-laying, which is a strong predictor of potential breeding success, was the same for 'Wadden Sea-stagers' and 'Baltic-stagers' (ch. 4). Apparently, by their large-scale change in site use the geese have managed to spread optimally over the total of resources available to them in the North Sea-Baltic

region during spring thereby escaping negative effects of density dependence. The hitherto unbroken geometric growth of the Russian barnacle goose population corroborates these findings.

During the pre-laying period upon arrival in the colony the geese seem to maintain the level of body stores, as has been concluded from their abdominal profile indices (Eichhorn unpubl. data)(for an evaluation of this method see Madsen and Klaassen 2006). Females deplete their body stores at a rate of 11 g d^{-1} over 25 days of incubation. At hatch they have reached their lowest body mass within the annual cycle (1500 g, ch. 7). Food availability peaks around hatch, allowing them to replenish stores quickly. After only 14 days from hatch females enter wing moult with a body mass similar to that at start of incubation (1720 g and 1742 g, respectively). This translates into a rate of body mass gain (since completion of incubation) of 19 g d^{-1}. The duties of rearing young (brooding and defence from predators) may be responsible for a lower gain rate compared to the spring staging period on Kanin which represents the peak value in the annual cycle (Fig. 8.2).

From arctic to temperate-breeding geese: comparison of major life-history traits

Clutch and incubation

For arctic-breeding barnacle geese poor food availability upon arrival in the colony and during egg-laying (a total period of ca. nine days) is expected to constrain both opportunities for replenishment of stores as well as clutch size. In contrast, temperate-breeding barnacle geese enjoy higher food availability at the time of egg-laying. Therefore, temperate geese can exploit current diet to produce eggs to a greater degree, thereby sparing body stores, than their arctic-breeding counterparts. This combined with smaller stores in migratory geese at the time of egg-laying due to costs of transport is the most likely explanation for the pattern of decreasing clutch size with latitude (ch. 7).

Most of the stored 'capital' brought by geese to their arctic breeding grounds is needed to sustain them through incubation (ch. 5). Surprisingly, the contribution of endogenous stores to incubation was even higher in temperate-breeding geese (ch. 7). Although different nest attentiveness may be the proximate reason for this (Box C), causes for higher nest attentiveness in temperate birds remain to be explained.

Timing of reproduction and moult

Despite an impressive advance of six to seven weeks in laying date compared to arctic breeders temperate barnacle geese breed too late in order to match peak food resources with growth of their young (ch. 6). Selection for earlier breeding is strong. But what are the prospects for improvement of the timing of reproduction? The ongoing amelioration of climate will advance the food peak further. Geese may be able to gain breeding condition earlier as well. However, there are limitations doing so. While climate change will affect food conditions, it will not affect light

regime. Therefore, geese would have to gain condition within increasingly shorter daylight periods which may confront them with a food-processing bottleneck (Sedinger and Raveling 1988; Prop and Vulink 1992). Thus, the mismatch will remain as long as both adults preparing for breeding and offspring depend on the same food peak. A broader diet including food sources peaking differently or migration between peaks offer possible evolutionary solutions to this dilemma.

Avian circannual rhythms are often controlled by an endogenous clock (Gwinner 1996) and this has been shown also for the timing of reproduction and wing moult in geese (Davies et al. 1969; Larsson 1996; Loonen and Follestad 1997). Interestingly, timing of wing moult has been considerably less advanced than reproduction in temperate-breeding barnacle geese compared to arctic breeders (ch. 6) indicating that these two cycles can be adjusted to new circumstances independently. Gwinner and Dorka (1976) revealed such an ability of birds to uncouple cycles of reproduction and moult in laboratory experiments with garden warblers *Sylvia borin*.

Post-fledging survival and the costs of migration

In the long-distance migrating Barents Sea population, post-fledging survival (i.e., survival from fledging in the arctic until arrival on the wintering grounds) was much lower (averaging 0.55) than in both the Baltic population (0.90) with its more modest migratory distance and the resident North Sea population (0.97)(ch. 6). Moreover, in the Barents Sea population there was a strong penalty for young that fledge late. Post-fledging survival in the Spitsbergen-breeding population of the barnacle goose was on average 0.84 in 'normal' seasons but fell to 0.65 in a late season (Owen and Black 1989). Hunting has been banned along the route taking this population via Norway to wintering grounds in Scotland. Taken together these comparisons implicate a higher mortality during autumn migration in the arctic populations, facing both long flights over open sea as well as hunting mortality.

However, if we consider the output of fledged young per nesting female that reach the winter grounds a comparison with data for the Spitsbergen population is again revealing. Prop and De Vries (1993, refined in Black et al. 2007) assessed the number of goslings surviving migration to Scotland per marked individual female in relation to the date they settled in the breeding colony. In the three early seasons in their material these values peak at approximately 1.5 surviving goslings for females settling between 2 and 8 June, with much lower success both earlier and later than this. Including the two late seasons in the study (0.3 goslings per female at best with little seasonal trend) the overall output was 0.55 ± 1.045 (SD) surviving goslings per female (n=335; J. Prop pers. comm.). This mean value compares with 0.42 for our Barents Sea population and 0.71 for the Baltic and 0.51 for the North Sea populations (ch. 6). In this comparison the North Sea population performs unexpectedly bad, given the very high post-fledging survival and large clutches (ch. 6, 7). This implies that many of the eggs laid by Dutch breeders do not produce a fledgling. Further research has to reveal the factors causing these losses.

It should be noted that these production values for 'goslings per breeding female' do not reflect the output for the population as a whole, as non-breeding is

not covered. These comparative figures also suggest that the proportion of non-breeders is likely to be higher in the arctic populations which are exposed to generally harsher environmental conditions. If they miss the very tight time window for laying a clutch (with a reasonable chance to produce offspring), they better refrain from breeding in that season altogether. Thus, for the population as a whole the non-migratory population breeding in the Netherlands performs very well and is growing at a spectacular rate of 23% annually since 1984 (Black et al. 2007). In part this may be an effect of relaxed density dependence in these still young colonies. Growth will inevitably slow down with saturation of suitable habitat, as has been recently observed for the Baltic breeding population which showed an annual growth of 11% over the period1984-2002 but is facing a decline currently (ch. 6). The Russian population has been increasing at an annual rate of 8% since 1975 (Black et al. 2007), so using this criterion the current balance of costs and benefits of arctic versus temperate breeding in this species obviously favours the latter.

Predation and facilitation by man

Reasons for the strong increase of the total barnacle goose population and the expansion of its breeding range have been addressed in several studies (Ebbinge 1991; Syroechkovsky 1995; Van Eerden et al. 2005; van der Graaf et al. 2006a; ch. 6 this thesis) with the general conclusion that reduced predation and disturbance over the entire range together with improved feeding conditions in the wintering

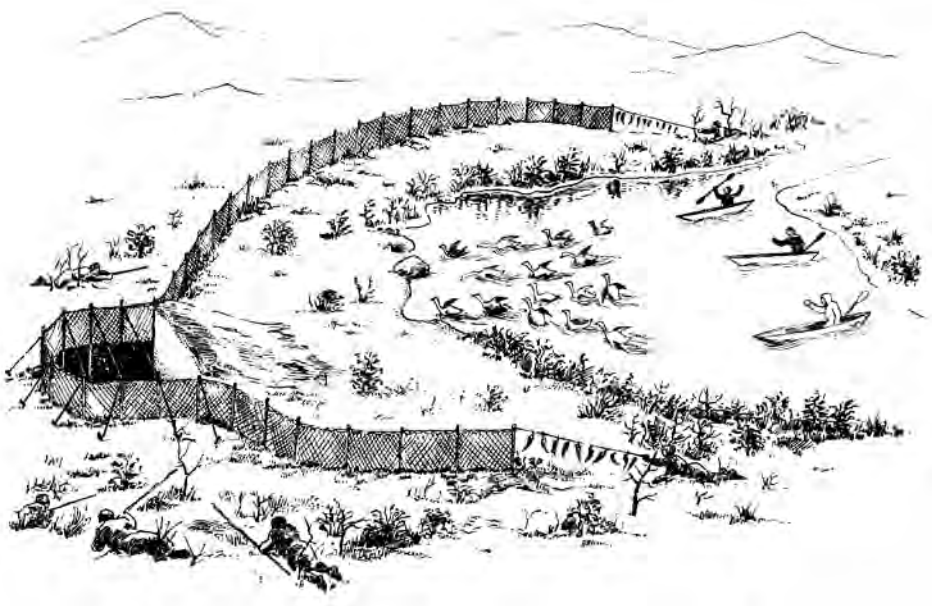

Figure 8.3. Siberian Dolgans driving flightless geese for capture (from Popov 1937). This drawing illustrates nicely the simple way we too caught moulting geese during this study (Note, we did not alter ground levels in or around the corral, in contrast to the catching construction illustrated here.).

area due to changes in agricultural practice must be regarded as the main drivers behind these changes. An increasing use of agricultural crop by geese and the positive effect on their numbers has been reported for most of the goose species in the northern hemisphere (Vickery and Gill 1999; Abraham et al. 2005; Gauthier et al. 2005; Fox et al. 2005).

Before the dramatic range expansion in recent times the Russian barnacle goose population was restricted to hardly accessible breeding sites on the islands of Novaya Zemlya and Vaygach and counted less than 20000 individuals 50 years ago (Ganter et al. 1999). These High Arctic strongholds may well have served as the only refuges left after times of intensive exploitation. Geese and other waterfowl are exceptional vulnerable when adults moult their wings and young have still to fledge. They can be captured easily and in great numbers during this flightless period (Nowak 1995; Fig. 8.3). Gathering highly nutritious food by such simple means has certainly a long-standing history among human hunting traditions (Trevor-Battye 1895). Reduced prosecution and predation may sufficiently explain the range expansion within the Arctic (Van der Graaf 2006). However, the establishment of temperate-breeding populations most likely required an improvement of local feeding conditions in addition (ch. 6). Without doubt, man has clearly an enormous impact on the dynamics of goose populations by both direct and indirect means (Jefferies and Drent 2006).

Fat or protein: distinguishing body composition during deposition and depletion

Some important conclusions in this thesis hinge upon our ability to distinguish between fat and protein components of the body (ch. 7, Box D; expanded here). Although total body water measurements by isotope dilution only allow estimates of the total lean mass, changes in wet lean mass over time can be almost entirely attributed to changes in wet protein mass while relative changes of other components like carbohydrates and minerals are regarded negligible. Fat and protein differ largely in energetic value and the roles they play in the organism. Fat binds about eight times more energy per unit wet mass than protein or carbohydrates and represents the major energy storage in birds (Blaxter 1989; Blem 1990). Protein has mainly structural and nutritional functions. Structural protein (e.g., muscles) can be mobilised to supply nutrients, for instance, for egg production (Nager 2006) or during immune responses (Klasing 2004). Only under extreme conditions and when fat reserves are exhausted, protein may temporarily serve as primary energy source (Blem 1990).

Depletion of stores

In chapter 7 we demonstrated the different composition of body mass (BM) lost during incubation in arctic versus temperate breeding barnacle geese, translating to energy contents of 34.9 kJ and 21.1 kJ per 1 g depleted BM, respectively. Spaans et

al. (2007) compiled energetic equivalents of BM loss during starvation for five bird species (including domestic goose and common eider *Somateria mollissima*) ranging from 20 to 25.9 kJ g^{-1}. Our value for temperate breeding barnacle geese fits into this range, indicating that, although the geese took feeding recesses (Box C), food intake was insufficient to balance endogenous protein loss. In contrast, arctic barnacle geese conserved protein by enhanced feeding during incubation. Thus, food uptake modifies the composition of the depleted body stores. This has implications for studies deriving energetic estimates from BM changes alone, which may or may not reflect true starvation. Until changes in body composition during incubation in brent geese *Branta bernicla* have been determined empirically (preferably by isotopic dilution), we will be in the dark regarding the extent these high arctic breeders draw on their protein reserves at this time (Spaans et al. 2007).

Deposition of stores and the boon or bane of 'agrifood'

Long-distance migrants such as the barnacle goose accumulate both protein and fat stores during spring, traditionally termed 'spring fattening' (Lindström and Piersma 1993; Prop and Black 1998). There are three approaches to discriminating between these two components: (1) carcass analysis (2) isotope dilution and (3) field studies on food intake and digestibility. Prop and Black (1998) applied method (3) for barnacle geese of the Spitsbergen population at a late spring staging site in Norway covering events in early May (2-3 weeks), and give an overview (their table 8) of results achieved for other goose species by method (1). Prop and Black (1998) estimated fat/protein ratios of stores of 1.2 to 1.4 for geese staging in salt marshes (feeding mainly on *Festuca rubra*), which contrasted strongly with a ratio of 22.6 estimated for geese feeding on improved agricultural grassland. I employed method (2) at a spring staging site in the Wadden Sea (Baltic-Russian barnacle goose population) from mid-March until the close of April. I estimated a fat/protein ratio of 8.1 to 13.0 and found no difference in the composition of geese utilising either agricultural pastures or natural saltmarshes (Box D).

The contrast in protein accumulation on agricultural versus saltmarsh habitat found by Prop and Black (1998) has been recently extended to spring staging brent geese in the Wadden Sea area (Prop and Spaans 2004, method 3). The nitrogen content (regarded to reflect protein content) and protein digestibility of pasture forage is often higher than of food plants from the salt marsh (Van der Jeugd et al. 2001; Bos and Stahl 2003; Prop and Spaans 2004). Birds excrete a mixture of faecal nitrogen (mainly from undigested food) and urinary nitrogen with their droppings, and it is important to distinguish between these sources in order to identify causes for differences in nitrogen (N) retention (Prop and Spaans 2004). In both studies by Prop and co-workers the lower nitrogen (N) retention in geese feeding on pastures was apparently not related to a depressed assimilation of N in the food but to a higher loss of urinary N. Figure 8.4 points at a similar pattern for spring staging barnacle geese in the Wadden Sea (island Schiermonnikoog): total N content in droppings is considerably higher for geese feeding on agricultural pastures compared to salt marshes, but the difference concerns mainly N from urinary waste products.

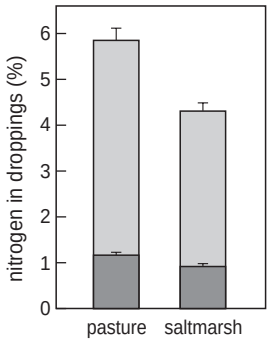

Figure 8.4. Nitrogen (N) partition in droppings of barnacle geese feeding in pasture or saltmarsh habitat in the Wadden Sea (Dutch island Schiermonnikoog) during spring. Total N contains faecal N (mainly originating from undigested food) shown in black and N from urinary waste products, shown as the remainder in grey (means plus SE, n=8 for each habitat). Faecal N was determined following a procedure based on Terpstra and De Hart (1974).

Why do geese make less use of the apparently higher protein content in pasture forage? And how can this be reconciled with similar body composition of barnacle geese captured in these two different feeding habitats in the Wadden Sea (Box D)?

One might argue that barnacle geese, captured on Schiermonnikoog's eastern salt marsh and pastureland, respectively, have integrated food from both habitats by frequently switching between them. During winter, pastures represent the only feeding habit for geese on the island. The salt marsh fills up quickly in goose numbers during February when food plants become available here too (Prins and Ydenberg 1985). Movement into salt marshes was enforced during years (before 2000) with goose scaring regimes on pastureland (Bos and Stahl 2003). However, switching birds have been seldom observed after the seasonal movement into the salt marsh (from March onwards) and individuals seem faithful to the chosen habitat (Van der Jeugd et al. 2001). Similarly, for brent geese on the island: intensive ring-reading of marked birds during May (when staging numbers peak) in two years yielded 28 rings in the pasture and 32 rings in the marsh, but none was observed in both habitats (Bos and Stahl 2003). A high site faithfulness within and between years was furthermore reported for brent geese staging on pastureland within an reserve on the Wadden Sea island of Texel (Spaans and Postma 2001). Although too limited to allow sound conclusions on food choice of barnacle geese on Schiermonnikoog, these data do not hint at feeding strategies integrating resources from both habitats over the short term.

Prop and Black (1998) and Prop and Spaans (2004) suspected a less favourable amino acid composition might be responsible for the lower nitrogen retention efficiency of geese feeding on pasture grass compared to those feeding in the salt marsh. Amino acids (aa) have to be digested in certain proportions, depending on actual requirements, in order to make the incorporation into body protein most effi-

cient. Most relevant here are the essential aa which cannot be synthesised from other metabolites within the body but have to be supplied by the diet. The balance of aa in the food is ideal when matching precisely the animal's requirements. In the concept of ideal aa ratios, the proportions of specific (essential) aa are expressed relative to lysine (Klasing 1998). Studies of dietary aa requirements are usually restricted to laboratory or farm animals. Thus, I relied on the ideal aa pattern established for growing broiler chicks by Baker (2003) and assume a similar aa balance for wild geese maximising protein deposition. The most limited dietary aa relative to requirements is called the first limiting aa. Lysine is usually regarded the first limiting aa in most (plant based) diets for animals during intensive protein accretion (Baker 2003; Boisen 2003).

Six major food plant species (nomenclature follows Van der Meijden 1996) utilised by spring staging barnacle and brent geese on Schiermonnikoog were sampled for amino acid analysis once in 2004 and again in 2005 (in both years between 1 and 4 May). The nearly sole food plant available in pastureland is *Lolium perenne* (amounts of *Poa pratense* being negligible). For barnacle geese in the salt marsh the staple diet is composed of *Festuca rubra* and *Juncus gerardi*, with *Festuca* alone contributing ca. 90% to the diet (Van Dinteren 1988; Van der Wal et al. 1998). Brent goose diet in the salt marsh consists mainly of *Puccinellia maritima* (70-80%) supplemented by *Festuca, Plantago maritima* and *Triglochin maritima* (Prop and Deerenberg 1991). Figure 8.5 depicts information about aa contents (as % dry weight) and about the balance of essential aa when adopting the ideal aa ratios established for the growing chicken (Baker 2003). Variation in amino acid contents is generally in line with variation in nitrogen content. Higher N contents in *Triglochin, Puccinellia* and *Lolium* are reflected in higher aa contents, and even at similar proportions for most of the aa but proline being a notable exception. *Triglochin* and *Puccinellia* are well known for their high accumulation of proline which functions as osmotic solute in these halophytes (Stewart and Lee 1974; Jefferies 1980). The high levels of (dietary dispensable) proline in food plants will largely be in excess of requirements by the animal, while the apparent value of essential aa will be smaller than expected from the higher total N content. For instance, *Triglochin* and *Puccinellia* had a, respectively, 33% and 11% higher total N content than *Lolium*, but the content of Lysine was elevated by, respectively, only 23% and 5% (Fig. 8.5).

Overall, differences in aa contents are small among the studied plant species. Furthermore, the relative proportions of aa are very similar for all plant samples and the same essential aa (and in similar proportions) are in excess or deficit of the assumed ideal pattern. Proportions of sulphur amino acids (saa) methionine, cystine and, to a small extent, arginine were smaller than expected from the ideal pattern. However, relative demand of saa in adult geese out of moult is likely lower than in growing chicks which have to synthesise much feather keratins. The great similarity of aa profiles in the six plant leaf samples is not surprising. Sedinger (1984) also found no major differences in aa patterns among goose forage plants in the Arctic, and relative proportions of specific aa remained constant over the season despite seasonal variation in total protein. He emphasised that 50-80% of leaf

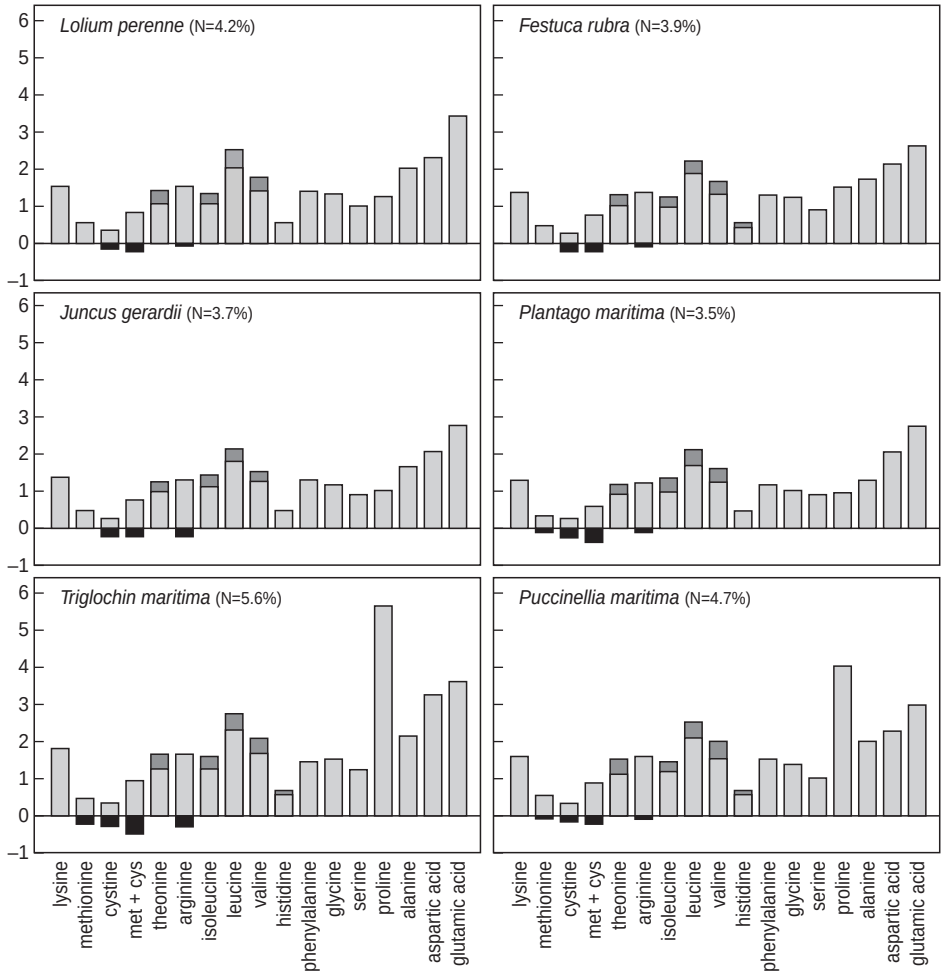

Figure 8.5. Amino acid (aa) contents (standardised to a dry matter content of 100%) in six plant species (average of two samples) are shown by positive values. The first 11 columns (from left to right) refer to essential aa (tryptophan was not measured), the last 6 columns to non-essential aa. For the essential aa (except phenylalanine) the measured contents were contrasted to expected contents according to ideal aa ratios established for growing broiler chicken (Baker 2003, see also text): proportions in excess of the ideal pattern are shown in dark grey; proportions in deficit are given as negative values in black colour. Columns for all non-essential aa and phenylalanine refer to the measured contents only. Nitrogen (N) contents measured in the same plant samples are given in brackets next to the plant species name.

protein is in the form of a single enzyme, ribulose biphosphate carboxylase (Rubisco), which may explain the relative invariance of aa ratios.

Thus, amino acid composition of food plants on the basis of our exploratory analyses cannot explain different nitrogen retention efficiencies in pasture and salt-

marsh feeding geese, and indeed I was unable to detect differences in the ratio of fat to protein deposited by barnacle geese utilising the two habitats in spring (Box D). The situation may differ when considering geese feeding on seeds of maize and other cereals (McLandress and Raveling 1981; Madsen 1985; Alisauskas and Ankney 1992b). Compared to grasses, cereal grains are a better energy source due to their higher content of carbohydrates and lipids, but the protein content is lower and proteins are deficient in certain essential aa, particularly lysine and methionine (McDonald et al. 1995). Geese relying primarily on grain in spring may thus encounter problems in accumulating protein stores in the body.

Instead of food plants' amino acid composition I propose an alternative reason for the relatively large proportion of urinary N excreted by geese feeding on pastureland (Fig. 8.4). N in forage comes, apart from proteins, from a variety of non-protein nitrogen (NPN) sources including free aa, nucleic acids, amides (e.g. urea, uric acid), amines, nitrates and further nitrogenous compounds (McDonald et al. 1995). Free aa can be present in substantial amounts like, for instance, much of the proline accumulated in certain halophytes (discussed above) and, as long as required, will be readily used for the building of body proteins. However, other assimilated NPN compounds cannot be used by geese for protein building and will enlarge the amount of urinary N. Thus, if these compounds are present in significant amounts, total food N should be corrected accordingly in order to calculate true protein retention efficiencies from nitrogen balances. Due to the intensive application of fertilisers many of these nitrogenous compounds may be particularly present in pasture grass, which is clearly the case for at least nitrate (Fig. 8.6). However, nitrate alone cannot explain all of the difference in N retention efficiencies, as nitrate N makes up only 2.5% of the total N in *Lolium*.

More research into the partitioning of N in food and faeces combined with feeding trials on different diets is required for a better understanding of nutritional limitations of protein acquisition and how this may relate to habitat utilisation in geese. Currently, geese all over the world seem to benefit from the exploitation of agricultural land. However, the continuing loss of their natural habitat and increasing dependence on agricultural crops renders geese 'captive of agricultural policy' (Jefferies and Drent 2006) and this may form a future bane to them, indeed.

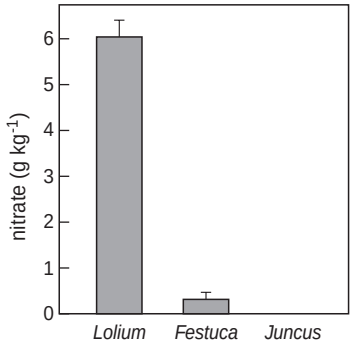

Figure 8.6. Nitrate content in three major food plants for barnacle geese staging on Schiermonnikoog: *Lolium perenne* in pastureland; *Festuca rubra* and *Juncus gerardi* in saltmarsh habitat. Nitrate content in *Juncus* was virtually zero.

Perspectives in the barnacle goose study

In Box D and above I discussed nutrient utilisation by geese staging in saltmarsh and agricultural habitat. A somewhat unresolved point concerned the question to what extent geese may integrate diet from both habitats. Direct observations of marked birds in an extensive area are difficult to record and provide only snapshots. Applications of advanced tracking techniques (e.g., radio-tracking and GPS) may provide accurate and frequent positions, and, combined with position/motion-sensitive gadgets, information on actual (feeding) behaviour of the animal (Hassall et al. 2001). Ideally, however, one would like to have a more direct measure of specific food usage by the individual. Comparison of signatures of stable isotopes in consumer tissue and potential food sources may prove very helpful to this end, including the assessment of temporal variation in diet (e.g., Hobson 2005; Dalerum and Angerbjörn 2005; Podlesak et al. 2005). For instance, (relatively non-invasive) blood sampling can already provide dietary information of two temporal periods: cellular and plasma fractions of blood have different metabolic turnover rates reflecting dietary intake over the past few weeks and past few days, respectively (Hobson and Clark 1993). Recently, Inger and co-workers (2006) applied this technique successfully in their study on dietary choice of brent geese utilising marine and agricultural habitat while wintering in Northern Ireland. A prerequisite is that isotopic signatures of different food sources must differ in order to quantify their relative contributions to an animal's diet (Phillips and Gregg 2001). Given the clear difference in nitrogen (and to a lesser extent carbon) stable isotope ratios between the major food plants from pastureland and salt-marsh habitat on Schiermonnikoog (Fig. 8.7) this technique would provide a suitable tool to infer resource usage by barnacle geese on the island.

Although some influence of ameliorated climate via food plants leading to better conditions cannot be excluded, other factors than climate change were regarded essentially responsible for the range expansion and change in migratory ecology of barnacle geese. This does not, however, automatically imply that the barnacle goose will have a low sensitivity to projected future climate change. Before any reasonable judgement is possible we would need to know more about the physiological adaptations allowing this species to breed in its former wintering area nowadays.

In particular the Arctic is now experiencing some of the most rapid and severe climate changes on earth, warming two to three times more rapidly than the global average, but also experiencing discontinuities (Høgda et al. 2001). Therefore, the Arctic is expected to be one of the most hard-hit environments on our globe (ACIA Integration Team 2005). To predict the impact of this unprecedented global change it is crucial to understand the mechanisms by which species adapt to environmental changes. Understanding these mechanisms also leads to more fundamental insights into how evolution proceeds towards different life histories.

Typically, Arctic breeding birds have high levels of energy metabolism (Klaassen 1994). This fast 'pace-of-life' is thought to be associated with the specific harsh conditions that are associated with living in a cold and highly seasonal environment

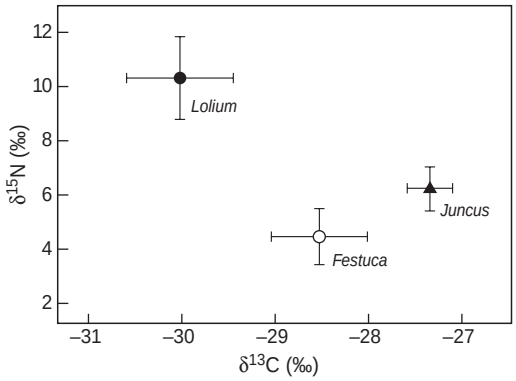

Figure 8.7. Comparison of nitrogen and carbon isotopic signatures of three food plants from two feeding habitats on Schiermonnikoog. Pasture forage consists to nearly 100% of *Lolium perenne*. Diet from the saltmarsh is mainly composed by *Festuca rubra* (ca. 90%) and *Juncus gerardi* (Van Dinteren 1988; Van der Wal et al. 1998).

(Klaassen and Drent 1991). At the same time it is hypothesised that the Arctic is a relatively germ-free environment, which would allow their inhabitants to reduce their immunological investments (Piersma 1997). Thus, one might expect life-history tradeoffs resulting from coupled physiological constraints like energy metabolism and immune function (Ricklefs and Wikelski 2002). Differences in metabolism-immune defence tradeoffs might reflect a phenotypic or genetic response or even a combination of both. The most powerful way to disentangle these processes is by means of translocation and common garden experiments. Recent findings using this approach confirm that immunological differences between populations of the same species are partly adaptive and perhaps genetic (Martin et al. 2004). These and other new insights from recent work on the avian 'pace-of-life' and its relationships with immune defence are predominantly based on comparisons of tropical resident versus temperate migrant or resident songbirds (Wikelski et al. 2003; Tieleman et al. 2005; Wiersma et al. 2007). It would be exciting to investigate if such concepts also apply to comparisons of temperate resident versus Arctic migrant birds, and to large, long-lived species that have a very different reproductive strategy and ontogeny compared to songbirds. The barnacle goose and its rapid range expansion along a north-south gradient provides a well suited study system for research on the mechanisms of adaptation and tradeoffs between lifestyles at different latitudes.

References

A

Abraham KF, Jefferies RL, Alisauskas RT (2005) The dynamics of landscape change and snow geese in mid-continent North America. Global Change Biology 11: 841-855

ACIA Integration Team (2005) Arctic Climate Impact Assessment - Scientific Report. Cambridge University Press, Cambridge

Aerts BA, Esselink P, Helder GJF (1996) Habitat selection and diet composition of greylag geese *Anser anser* and barnacle geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the Dollard. Zeitschrift für Ökologie und Naturschutz 5: 65-75

Afanasyev V (2004) A miniature daylight level and activity data recorder for tracking animals over long periods. Memoirs National Institute of Polar Research (Japan) Spec. Issue 58: 227-233

Afton AD, Paulus SL (1992) Incubation and brood care. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) Eology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, pp 62-108

Aldrich TW, Raveling DG (1983) Effects of experience and body weight on incubation behavior of Canada geese. Auk 100: 670-679

Alerstam T (2006a) Conflicting evidence about long-distance animal navigation. Science 313: 791-794

Alerstam T (2006b) Strategies for the transition to breeding in time-selected bird migration. Ardea 94: 347-357

Alerstam T, Hake M, Kjellen N (2006) Temporal and spatial patterns of repeated migratory journeys by ospreys. Animal Behaviour 71: 555-566

Alerstam T, Hedenström A (1998) The development of bird migration theory. Journal of Avian Biology 29: 343-369

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103: 247-260

Alerstam T, Hjort C, Högsted G, Jönsson PE, Karlsson J, Larsson B (1986) Spring migration of birds across the Greenland Inlandice. Meddelelser om Grønland, Bioscience 21: 1-38

Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E (ed) Bird Migration: Physiology and Ecophysiology. Springer-Verlag, Berlin, pp 331-351

Alisauskas RT, Ankney CD (1992a) Egg laying and nutrient reserves. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) Eology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, pp 30-61

Alisauskas RT, Ankney CD (1992b) Spring habitat use and diets of midcontinent adult lesser snow geese. Journal of Wildlife Management 56: 43-54

Allen LR, Hume ID (2001) The maintenance nitrogen requirement of the zebra finch *Taeniopygia guttata*. Physiological and Biochemical Zoology 74: 366-375

Alsos IG, Elvebakk A, Gabrielsen GW (1998) Vegetation exploitation by barnacle geese *Branta leucopsis* during incubation on Svalbard. Polar Research 17: 1-14

Amat JA (1995) Effects of wintering greylag geese *Anser anser* on their *Scirpus* food plants. Ecography 18: 155-163

Anderson DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64: 912-923

Ankney CD (1984) Nutrient reserve dynamics of breeding and molting brant. Auk 101: 361-370

Ankney CD, MacInnes CD (1978) Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95: 459-471

Anonymous (1996) Southern Barents Sea and Beloye More Pilot. UK Hydrographic Office, HMSO, pp 1-166

Ar A, Sidis Y (2002) Nest microclimate during incubation. In: Deeming DC (ed) Avian Incubation: Behaviour, Environment and Evolution. Oxford University Press, Oxford, pp 143-160

Arnould JPY, Boyd IL, Speakman JR (1996) Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): validation of hydrogen isotope dilution. Physiological Zoology 69: 93-116

Arzel C, Elmberg J, Guillemain M (2006) Ecology of spring-migrating *Anatidae*: a review. Journal of Ornithology 147: 167-184

Austin JE, Fredrickson LH (1987) Body and organ mass and body composition of post-breeding female lesser scaup. Auk 104: 694-699

B

Badyaev AV, Hill GE, Beck ML, Dervan AA, Duckworth RA, McGraw AJ, Nolan PM, Whittingham LA (2002) Sex-biased hatching order and adaptive population divergence in a passerine bird. Science 295: 316-318

Badyaev AV, Martin TE (2000) Sexual dimorphism in relation to current selection in the house finch. Evolution 54: 987-997

Bairlein F, Gwinner E (1994) Nutritional mechanisms and temporal control of migratory energy accumulation in birds. Annual Review of Nutrition 14: 187-215

Baker AJ, Gonzalez PM, Piersma T, Niles LJ, do Nascimento IDS, Atkinson PW, Clark NA, Minton CDT, Peck MK, Aarts G (2004) Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proceedings of the Royal Society of London Series B 271: 875-882

Baker DH (2003) Ideal amino acid patterns for broiler chicks. In: D'Mello JPF (ed) Amino Acids in Animal Nutrition. CAB International, Wallingford, UK, pp 223-235

Barboza PS, Jorde DG (2002) Intermittent fasting during winter and spring affects body composition and reproduction of a migratory duck. Journal of Comparative Physiology B 172: 419-434

Barry TW (1962) Effects of late seasons on Atlantic brant reproduction. Journal of Wildlife Management 26: 19-26

Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) (1992) Eology and Management of breeding waterfowl. University of Minnesota Press, Minneapolis

Battley PF (2006) Consistent annual schedules in a migratory shorebird. Biology Letters 2: 517-520

Battley PF, Piersma T (1997) Body composition of lesser knots *Calidris canutus* rogersi preparing to take off on migration from northern New Zealand. Notornis 44: 137-150

Battley PF, Piersma T, Rogers DI, Dekinga A, Spaans B, Van Gils JA (2004) Do body condition and plumage during fuelling predict northwards departure dates of great knots *Calidris tenuirostris* from north-west Australia? Ibis 146: 46-60

Bech C, Østnes JE (1999) Influence of body composition on the metabolic rate of nestling European shags (*Phalacrocorax aristotelis*). Journal of Comparative Physiology B 169: 263-270

Béchet A, Giroux JF, Gauthier G (2004) The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. Journal of Applied Ecology 41: 689-700
Benson AM, Winker K (2005) Fat-deposition strategies among high-latitude passerine migrants. Auk 122: 544-557
Berthold P, Helbig AJ, Mohr G, Querner U (1992) Rapid microevolution of migratory behaviour in a wild bird species. Nature 360: 668-670
Berthold P, Kaatz M, Querner U (2004) Long-term satellite tracking of white stork (Ciconia ciconia) migration: constancy versus variability. Journal of Ornithology 145: 356-359
Berthold P, von der Bossche W, Jakubiec Z, Kaatz C, Kaatz M, Querner U (2002) Long-term satellite tracking sheds light upon variable migration strategies of white storks (*Ciconia ciconia*). Journal für Ornithologie 143: 489-493
Bêty J, Gauthier G, Giroux JF (2003) Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. American Naturalist 162: 110-121
Bêty J, Giroux JF, Gauthier G (2004) Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behavioral Ecology and Sociobiology 57: 1-8
Black JM (ed) (1996) Partnerships in Birds: The Study of Monogamy. Oxford University Press, Oxford
Black JM, Prop J, Larsson K (2007) Wild Goose Dilemmas. Branta Press, Groningen
Blaxter KL (1989) Energy Metabolism in Animals and Man. Cambridge University Press, Cambridge
Blem CR (1990) Avian energy storage. In: Power DM (ed) Current Ornithology. Plenum Press, New York, pp 59-113
Boisen S (2003) Ideal dietary amino acid profiles for pigs. In: D'Mello JPF (ed) Amino Acids in Animal Nutrition. CAB International, Wallingford, UK, pp 157-168
Boismenu C, Gauthier G, Larochelle J (1992) Physiology of prolonged fasting in greater snow geese (*Chen caerulescens atlantica*). Auk 109: 511-521
Bolduc F, Guillemette M (2003) Incubation constancy and mass loss in the common eider *Somateria mollissima*. Ibis 145: 329-332
Boos M, Zorn T, Koch A, Le Maho Y, Robin JP (2000) Determining body fuels of wintering mallards. Comptes rendus de l'Académie des sciences Série III, Sciences de la vie 323: 183-193
Bos D, Stahl J (2003) Creating new foraging opportunities for dark-bellied brent *Branta bernicla* and barnacle geese *Branta leucopsis* in spring: insights from a large-scale experiment. Ardea 91: 153-165
Bos D, Van der Koppel J, Weissing FJ (2004) Dark-bellied brent geese aggregate to cope with increased levels of primary production. Oikos 107: 485-496
Both C (2007) Comment on "Rapid advance of spring arrival dates in long-distance migratory birds". Science 315: 598b
Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 441: 81-83
Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 296-298
Botta A, Viovy N, Ciais P, Friedlingstein P, Monfray P (2000) A global prognostic scheme of leaf onset using satellite data. Global Change Biology 6: 709-725
Bowler J (2005) Breeding strategies and biology. In: Kear J (ed) Ducks, Geese and Swans. Oxford University Press, pp 68-111
Brinkhof MWG, Cave AJ, Daan S, Perdeck AC (2002) Timing of current reproduction directly affects future reproductive output in European coots. Evolution 56: 400-411
Brinkhof MWG, Cave AJ, Hage FJ, Verhulst S (1993) Timing of reproduction and fledging success in the coot *Fulica atra*: evidence for a causal relationship. Journal of Animal Ecology 62: 577-587
Brown ME (1996) Assessing body condition in birds. In: Nolan V, Ketterson ED (eds) Current Ornithology. Plenum Press, New York, pp 67-135

Butler PJ, Bishop CM, Woakes AJ (2003) Chasing a wild goose: posthatch growth of locomotor muscles and behavioural physiology of migration of an Arctic goose. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian Migration. Springer-Verlag, Berlin Heidelberg, pp 527-542

Butler PJ, Woakes AJ, Bevan RM, Stephenson R (2000) Heart rate and rate of oxygen consumption during flight of the barnacle goose, *Branta leucopsis*. Comparative Biochemistry and Physiology A: Molecular & Integrative Physiology 126: 379-385

Butler PJ, Woakes AJ, Bishop CM (1998) Behaviour and physiology of Svalbard barnacle geese *Branta leucopsis* during their autumn migration. Journal of Avian Biology 29: 536-545

C

Calder WA, King JR (1974) Thermal and caloric relationships of birds. In: Farner DS, King JR (eds) Avian Biology, Vol. IV. Academic Press, New York, pp 259-413

Caloin M (2004) Modeling of lipid and protein depletion during total starvation. American Journal of Physiology-Endocrinology and Metabolism 287: E790-E798

Campbell RR, Leatherland JF (1980) Estimating body protein and fat from water content in lesser snow geese. Journal of Wildlife Management 44: 438-446

Carey C (ed) (1996a) Avian Energetics and Nutritional Ecology. Chapman & Hall, New York

Carey C (1996b) Female reproductive energetics. In: Carey C (ed) Avian Energetics and Nutritional Ecology. Chapman & Hall, New York, pp 324-374

Cartar RV, Morrison RIG (1997) Estimating metabolic costs for homeotherms from weather data and morphology: an example using calidridine sandpipers. Canadian Journal of Zoology 75: 94-101

Cherel Y, Robin JP, Heitz A, Calgari C, Le Maho Y (1992) Relationships between lipid availability and protein utilization during prolonged fasting. Journal of Comparative Physiology B 162: 305-313

Choiniere L, Gauthier G (1995) Energetics of reproduction in female and male greater snow geese. Oecologia 103: 379-389

Christians JK (2000) Trade-offs between egg size and number in waterfowl: an interspecific test of the van Noordwijk and de Jong model. Functional Ecology 14: 497-501

Clausen P, Green M, Alerstam T (2003) Energy limitations for spring migration and breeding: the case of brent geese *Branta bernicla* tracked by satellite telemetry to Svalbard and Greenland. Oikos 103: 426-445

Conradt L, Roper TJ (2005) Consensus decision making in animals. Trends in Ecology & Evolution 20: 449-456

Cooch EG, Lank DB, Dzubin A, Rockwell RF, Cooke F (1991) Body size variation in lesser snow geese: environmental plasticity in gosling growth rate. Ecology 72: 503-512

Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433: 513-516

Coyne MS, Godley BJ (2005) Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. Marine Ecology Progress Series 301: 1-7

Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. Nature 388: 526

Crum BG, Williams JB, Nagy KA (1985) Can tritiated water-dilution space accurately predict total-body water in chukar partridges? Journal of Applied Physiology 59: 1383-1388

Culebras JM, Moore FD (1977) Total body water and the exchangeable hydrogen. I. Theoretical calculation of non-aqueous exchangeable hydrogen in man. American Journal of Physiology 232: R54-R59

Cuthill IC, Houston AI (1997) Managing time and energy. In: Krebs JR, Davies NB (eds) Behavioural Ecology: An Evolutionary Approach. Blackwell Science, Oxford, pp 97-120

D

Daan S, Dijkstra C, Tinbergen JM (1990) Family planning in the kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. Behaviour 114: 83-116

Daan S, Tinbergen JM (1997) Adaptation of life histories. In: Krebs JR, Davis NB (eds) Behavioural Ecology: An Evolutionary Approach. Blackwell Science, Oxford, pp 311-333
Dalerum F, Angerbjörn A (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144: 647-658
Dalhaug L, Tombre IM, Erikstad KE (1996) Seasonal decline in clutch size of the barnacle goose in Svalbard. Condor 98: 42-47
Davidson NC (1984) Changes in the condition of dunlins and knots during short-term captivity. Canadian Journal of Zoology 62: 1724-1731
Davies C, Fischer H, Gwinner E (1969) Differences in breeding times between certain species of geese and their hybrids under identical conditions. Oecologia 3: 266-276
Dawson TJ, Whitehead PJ, McLean A, Fanning FD, Dawson WR (2000) Digestive function in Australian magpie geese (*Anseranas semipalmata*). Australian Journal of Zoology 48: 265-279
Degen AA, Pinshow B, Alkon PU, Arnon H (1981) Tritiated water for estimating total body water and water turnover rate in birds. Journal of Applied Physiology 51: 1183-1188
Delany S, Scott D (eds) (2002) Waterbird Population Estimates, 3rd edition. Wetlands International Global Series 12. Wetlands International, Wageningen
Dietz MW, Piersma T, Dekinga A (1999) Body-building without power training? Endogenously regulated pectoral muscle hypertrophy in confined shorebirds. Journal of Experimental Biology 202: 2831-2837
Drent R, Both C, Green M, Madsen J, Piersma T (2003) Pay-offs and penalties of competing migratory schedules. Oikos 103: 274-292
Drent R, Weijand B, Ebbinge B (1978) Balancing the energy budget of arctic breeding geese throughout the annual cycle: a progress report. Verhandlungen der Ornithologischen Gesellschaft in Bayern 23: 239-264
Drent RH (2006) The timing of birds' breeding seasons: the Perrins hypothesis revisited especially for migrants. Ardea 94: 305-322
Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252
Drent RH, Eichhorn G, Flagstad A, Van der Graaf AJ, Litvin KE, Stahl J (2007) Migratory connectivity in Arctic geese: spring stopovers are the weak links in meeting targets for breeding. Journal of Ornithology 148: S501-S514
Drent RH, Fox AD, Stahl J (2006) Travelling to breed. Journal of Ornithology 147: 122-134
Dunn EH, MacInnes CD (1987) Geographic variation in clutch size and body size of Canada geese. Journal of Field Ornithology 58: 355-371

E

Ebbinge BS (1991) The impact of hunting on mortality rates and spatial distribution of geese wintering in the Western Palearctic. Ardea 79: 197-209
Ebbinge BS (1992) Regulation of numbers of dark-bellied brent geese *Branta bernicla bernicla* on spring staging sites. Ardea 80: 203-228
Ebbinge BS, Spaans B (1995) The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the High Arctic. Journal of Avian Biology 26: 105-113
Ebbinge BS, Van Biezen JB, Van der Voet H (1991) Estimation of annual adult survival rates of barnacle geese *Branta leucopsis* using multiple resightings of marked individuals. Ardea 79: 73-112
Eichholz MW, Sedinger JS (1999) Regulation of incubation behavior in black brant. Canadian Journal of Zoology 77: 249-257
Eichhorn G (2005) Northward bound: fat for flight. How barnacle geese budget their spring travels. In: Drent RH, Tinbergen JM, Bakker JP, Piersma T (eds) Seeking Nature's Limits. KNNV Publishing, Utrecht, pp 102-113
Eichhorn G, Afanasyev V, Drent RH, Van der Jeugd HP (2006) Spring stopover routines in Russian barnacle geese *Branta leucopsis* tracked by resightings and geolocation. Ardea 94: 667-678

Eichhorn G, Visser GH (2008, *in press*) Evaluation of the deuterium dilution method to estimate body composition in the barnacle goose: accuracy and minimum equilibration time.

Ekstrom PA (2004) An advance in geolocation by light. Memoirs National Institute of Polar Research (Japan) Spec. Issue 58: 210-226

Ellis HI, Jehl JR (1991) Total body water and body composition in phalaropes and other birds. Physiological Zoology 64: 973-984

Elts J, Kuresoo A, Leibak E, Leito A, Lilleleht V, Luigujõe L, Lõhmus A, Mägi E, Ots M (2003) Status and numbers of Estonian birds, 1988-2002. Hirundo 16: 58-83

Erikstad KE, Bustnes JO, Moum T (1993) Clutch size determination in precocial birds - a study of the common eider. Auk 110: 623-628

Erikstad KE, Fauchald P, Tveraa T, Steen H (1998) On the cost of reproduction in long-lived birds: The influence of environmental variability. Ecology 79: 1781-1788

Erikstad KE, Tveraa T (1995) Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*? Oecologia 103: 270-274

Esler D, Grand JB (1994) The role of nutrient reserves for clutch formation by northern pintails in Alaska. Condor 96: 422-432

Esler D, Grand JB, Afton AD (2001) Intraspecific variation in nutrient reserve use during clutch formation by lesser scaup. Condor 103: 810-820

F

Falconer DS (1989) Introduction to Quantitative Genetics. Longman Scientific and Technical, New York

Figuerola J, Green AJ (2006) A comparative study of egg mass and clutch size in the *Anseriformes*. Journal of Ornithology 147: 57-68

Filchagov AV, Leonovich VV (1992) Breeding range expansion of barnacle and brent geese in the Russian European North. Polar Research 11: 41-46

Findlay CS, Cooke F (1982) Synchrony in the lesser snow goose (*Anser caerulescens caerulescens*). II. The adaptive value of reproductive synchrony. Evolution 36: 786-799

Forslund P, Larsson K (1991) The effect of mate change and new partner's age on reproductive success in the barnacle goose *Branta leucopsis*. Behavioral Ecology 2: 116-122

Forslund P, Larsson K (1992) Age-related reproductive success in the barnacle goose. Journal of Animal Ecology 61: 195-204

Forslund P, Larsson K (1995) Intraspecific nest parasitism in the barnacle goose: behavioural tactics of parasites and hosts. Animal Behaviour 50: 509-517

Forstmeier W (2002) Benefits of early arrival at breeding grounds vary between males. Journal of Animal Ecology 71: 1-9

Fox AD, Christian M, Alyn J (2003) Spring migration routes and timing of Greenland white-fronted geese - results from satellite telemetry. Oikos 103: 415-425

Fox AD, Madsen J, Boyd H, Kuijken E, Norriss DW, Tombre IM, Stroud DA (2005) Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. Global Change Biology 11: 881-893

G

Gabrielsen GW, Mehlum F, Karlsen HE, Andresen O, Parker E (1991) Energy cost during incubation and thermoregulation in the female common eider *Somateria mollissima*. Norsk Polarinstitutt Skrifter 195: 51-62

Galef B, Heyes CM (2004) Social learning and imitation. Learning and Behaviour (special issue) 32: 1-140

Ganter B, Cooke F (1996) Pre-incubation feeding activities and energy budgets of snow geese: Can food on the breeding grounds influence fecundity? Oecologia 106: 153-165

Ganter B, Larsson K, Syroechkovsky E.V., Litvin KE, Leito A, Madsen J (1999) Barnacle goose *Branta leucopsis*: Russian and Baltic populations. In: Madsen J, Fox AD, Cracknell J (eds) Goose Populations of the Western Palearctic. A Review of Status and Distribution. Wetlands International, Wageningen, pp 270-283

Garrettson PR, Rohwer FC (1998) Reproductive effort and survival of wild blue-winged teal,

Anas discors, with backpack harness and implant transmitters. Canadian Field-Naturalist 112: 212-216
Garrettson PR, Rohwer FC, Moser EB (2000) Effects of backpack and implanted radiotransmitters on captive blue-winged teal. Journal of Wildlife Management 64: 216-222
Gauthier G, Bêty J, Hobson KA (2003) Are greater snow geese capital breeders? New evidence from a stable-isotope model. Ecology 84: 3250-3264
Gauthier G, Giroux JF, Bedard J (1992) Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. Canadian Journal of Zoology 70: 2077-2087
Gauthier G, Giroux JF, Reed A, Béchet A, Belanger L (2005) Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands? Global Change Biology 11: 856-868
Gehre M, Geilmann H, Richter J, Werner RA, Brand WA (2004) Continuous flow $^{2}H/^{1}H$ and $^{18}O/^{16}O$ analysis of water samples with dual inlet precision. Rapid Communications in Mass Spectrometry 18: 2650-2660
Gessaman JA (1999) Evaluation of some non-lethal methods of estimating avian body fat and lean mass. In: Adams N, Slotow R (eds) Proceedings of the 22nd International Ornithological Congress. Durban University of Natal Press, Durban, South Africa, pp 2-16
Gill JA, Norris K, Potts PM, Gunnarsson TG, Atkinson PW, Sutherland WJ (2001) The buffer effect and large-scale population regulation in migratory birds. Nature 412: 436-438
Glahder CM, Fox AD, Hübner CE, Madsen J, Tombre IM (2006) Pre-nesting site use of satellite transmitter tagged Svalbard pink-footed geese *Anser brachyrhynchus*. Ardea 94: 679-690
Gloutney ML, Clark RG (1991) The significance of body mass to female dabbling ducks during late incubation. Condor 93: 811-816
Green M (1998) Spring migration of Barnacle Goose *Branta leucopsis* and Dark-bellied Brent Goose *B. bernicla bernicla* over Sweden. Ornis Svecica 8: 103-123
Green M, Alerstam T, Clausen P, Drent R, Ebbinge BS (2002) Dark-bellied Brent Geese *Branta bernicla bernicla*, as recorded by satellite telemetry, do not minimize flight distance during spring migration. Ibis 144: 106-121
Grieco F, Van Noordwijk AJ, Visser ME (2002) Evidence for the effect of learning on timing of reproduction in blue tits. Science 296: 136-138
Groscolas R, Schreiber L, Morin F (1991) The use of tritiated water to determine protein and lipid utilization in fasting birds: a validation-study in incubating Great-winged Petrels, *Pterodroma macroptera*. Physiological Zoology 64: 1217-1233
Guan J, Xiang P, Keating XD (2004) Evaluating the replicability of sample results: a tutorial of double cross-validation methods. Measurement in physical education and exercise science 8: 227-241
Gudmundsson GA, Lindström Å, Alerstam T (1991) Optimal Fat Loads and Long-Distance Flights by Migrating Knots Calidris-Canutus, Sanderlings C-Alba and Turnstones Arenaria-Interpres. Ibis 133: 140-152
Gunnarsson TG, Gill JA, Atkinson PW, Gelinaud G, Potts PM, Croger RE, Gudmundsson GA, Appleton GF, Sutherland WJ (2006) Population-scale drivers of individual arrival times in migratory birds. Journal of Animal Ecology 75: 1119-1127
Gurtovaya EN (1997) Breeding conditions for barnacle geese on Vaygach Island in 1996. Casarca: 109-110
Gwinner E (1996) Circannual clocks in avian reproduction and migration. Ibis 138: 47-63
Gwinner E, Dorka V (1976) Endogenous control of annual reproductive rhythm in birds. Proceedings of the 16th International Ornithological Congress: 223-234

H

Hallanaro E-L, Pylvänäinen M (2002) Nature in Northern Europe - Biodiversity in a changing environment. Nord 2001: 13, Nordic Council of Ministers, Copenhagen
Hanssen SA (2006) Costs of an immune challenge and terminal investment in a long-lived bird. Ecology 87: 2440-2446

Hanssen SA, Hasselquist D, Folstad I, Erikstad KE (2004) Costs of immunity: immune responsiveness reduces survival in a vertebrate. Proceedings of the Royal Society of London Series B 271: 925-930

Hanssen SA, Hasselquist D, Folstad I, Erikstad KE (2005) Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. Proceedings of the Royal Society of London Series B 272: 1039-1046

Hassall M, Lane SJ, Stock M, Percival SM, Pohl B (2001) Monitoring feeding behaviour of brent geese *Branta bernicla* using position-sensitive radio transmitters. Wildlife Biology 7: 77-86

Hedenström A (2007) Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society B doi: 10.1098/rstb.2007.2140

Helm B, Gwinner E (2005) Carry-over effects of day length during spring migration. Journal of Ornithology 146: 348-354

Helm B, Piersma T, Van der Jeugd HP (2006) Sociable schedules: interplay between avian seasonal and social behaviour. Animal Behaviour 72: 245-262

Hepp GR, Kennamer RA, Harvey WF (1990) Incubation as a reproductive cost in female wood ducks. Auk 107: 756-764

Hik DS, Jefferies RL (1990) Increases in the net aboveground primary production of a salt marsh forage grass: a test of the predictions of the herbivore-optimization model. Journal of Ecology 78: 180-195

Hill RD (1994) Theory of geolocation by light levels. In: Le Boeuf BJ, Laws RM (eds) Elephant Seals: Population Ecology, Behaviour and Physiology. University of California Press, Berkeley, pp 227-236

Hobson KA (2003) Making migratory connections with stable isotopes. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian Migration. Springer-Verlag, Berlin Heidelberg, pp 379-391

Hobson KA (2005) Using stable isotopes to trace long-distance dispersal in birds and other taxa. Diversity and Distributions 11: 157-164

Hobson KA (2006) Using stable isotopes to quantitatively track endogenous and exogenous nutrient allocations to eggs of birds that travel to breed. Ardea 94: 359-369

Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for non-destructive sampling in avian dietary studies. Auk 110: 638-641

Hochachka W (1990) Seasonal decline in reproductive-performance of song sparrows. Ecology 71: 1279-1288

Høgda KA, Karlsen SR, Solheim I (2001) Climate change impact on growing season in Fennoscandia studied by a time series of NOAA AVHRR NDVI data. Proceedings IGARSS 2001. 9-13 July 2001, Sydney, Australia.

Hohman WL, Ankney CD, Gordon DH (1992) Ecology and management of postbreeding waterfowl. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) Eology and Management of breeding waterfowl. University of Minnesota Press, Minneapolis, pp 128-189

Houston AI, Stephens PA, Boyd IL, Harding KC, McNamara JM (2007) Capital or income breeding? A theoretical model of female reproductive strategies. Behavioral Ecology 18: 241-250

Hübner CE (2006) The importance of pre-breeding areas for the arctic barnacle goose *Branta leucopsis*. Ardea 94: 701-713

Hughes MR, Roberts JR, Thomas BR (1987) Total body water and its turnover in free-living nestling glaucous-winged gulls with a comparison of body water and water flux in avian species with and without salt glands. Physiological Zoology 60: 481-491

Hupp JW, Pearce JM, Mulcahy DM, Miller DA (2006a) Effects of abdominally implanted radiotransmitters with percutaneous antennas on migration, reproduction, and survival of Canada geese. Journal of Wildlife Management 70: 812-822

Hupp JW, Schmutz JA, Ely CR (2006b) The prelaying interval of emperor geese on the Yukon-Kuskokwim Delta, Alaska. Condor 108: 912-924

Hupp JW, Ruhl GA, Pearce JM, Mulcahy DM, Tomeo MA (2003) Effects of implanted radio transmitters with percutaneous antennas on the behavior of Canada geese. Journal of Field Ornithology 74: 250-256

Hutchinson AE, Owen RB (1984) Bone-marrow fat in waterfowl. Journal of Wildlife Management 48: 585-591

I

Inger R, Ruxton GD, Newton J, Colhoun K, Robinson JA, Jackson AL, Bearhop S (2006) Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. Journal of Animal Ecology 75: 1190-1200

IPCC (2001) Climate Change 2001: Synthesis Report. A contribution of working groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

J

Jamieson SE, Gilchrist HG, Merkel FR, Falk K, Diamond AW (2006) An evaluation of methods used to estimate carcass composition of common eiders *Somateria mollissima*. Wildlife Biology 12: 219-226

Jefferies RL (1980) The role of organic solutes in osmoregulation in halophytic higher plants. In: Rains DW, Valentine RC, Hollaender A (eds) Genetic Engineering of Osmoregulation. Plenum Press, New York, pp 135-154

Jefferies RL, Drent RH (2006) Arctic geese, migratory connectivity and agricultural change: calling the sorcerer's apprentice to order. Ardea 94: 537-554

Jefferies RL, Drent RH, Bakker JP (2006) Connecting Arctic and temperate wetlands and agricultural landscapes: the dynamics of goose populations in response to global change. In: Verhoeven JTA, Beltman B, Bobbink R, Whigham DF (eds) Wetlands and Natural Resource Management. Ecological Studies Vol. 190. Springer-Verlag, Berlin Heidelberg, pp 293-314

Johnson DH, Nichols JD, Schwartz MD (1992) Population dynamics of breeding waterfowl. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) Eology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, pp 446-485

Jonsson JE, Afton AD, Alisauskas RT (2007) Does body size influence nest attendance? A comparison of Ross's geese (Chen rossii) and the larger, sympatric lesser snow geese (*C. caerulescens caerulescens*). Journal of Ornithology 148: 549-555

Jonzén N, Lindén A, Ergon T, Knudsen E, Vik JO, Rubolini D, Piacentini D, Brinch C, Spina F, Karlsson L, Stervander M, Andersson A, Waldenström J, Lehikoinen A, Edvardsen E, Solvang R, Stenseth NC (2006) Rapid advance of spring arrival dates in long-distance migratory birds. Science 312: 1959-1961

Jonzén N, Lindén A, Ergon T, Knudsen E, Vik JO, Rubolini D, Piacentini D, Brinch C, Spina F, Karlsson L, Stervander M, Andersson A, Waldenström J, Lehikoinen A, Edvardsen E, Solvang R, Stenseth NC (2007) Response to comment on "Rapid advance of spring arrival dates in long-distance migratory birds". Science 315: 598c

K

Kalyakin VN (1986) On the distribution and ecology of the barnacle goose on Vaygach Island and Yugorsky Peninsula. In: Ilyichev VD (ed) Actual Problems in Ornithology. Nauka, Moscow, pp 93-104

Kalyakin VN (2001) New data on bird fauna of Novaya Zemlya Archipelago and Franz Josef Land. Ornitologiya 29: 8-16

Kamp K, Preuss NO (2005) The greylag geese of Utterslev Mose – a long-term population study of wild geese in an urban setting. Dansk Ornitologisk Forenings Tidsskrift 99: 1-78

Klaassen M (1994) Growth and energetics of tern chicks from temperate and polar environments. Auk 111: 525-544

Klaassen M (2003) Relationships between migration and breeding strategies in arctic breeding birds. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian Migration. Springer-Verlag, Berlin Heidelberg, pp 237-249

Klaassen M, Bauer S, Madsen J, Tombre IM (2006a) Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. Journal of Applied Ecology 43: 92-100

Klaassen M, Abraham KF, Jefferies RL, Vrtiska M (2006b) Factors affecting the site of investment, and the reliance on savings for arctic breeders: the capital-income dichotomy revisited. Ardea 94: 371-384

Klaassen M, Drent R (1991) An analysis of hatchling resting metabolism - in search of ecological correlates that explain deviations from allometric relations. Condor 93: 612-629

Klaassen M, Lindström Å, Meltofte H, Piersma T (2001) Arctic waders are not capital breeders. Nature 413: 794

Klasing KC (1998) Comparative Avian Nutrition. CAB International, Wallingford

Klasing KC (2004) The costs of immunity. Acta Zoologica Sinica 50: 961-969

Klein Tank AMG, Wijngaard JB, Können GP, Böhm R, Demarée G, Gocheva A, Mileta M, Pashiardis S, Hejkrlik L, Kern-Hansen C, Heino R, Bessemoulin P, Müller-Westermeier G, Tzanakou M, Szalai S, Páalsdóttir T, Fitzgerald D, Rubin S, Capaldo M, Maugeri M, Leitass A, Bukantis A, Aberfeld R, Van Engelen AFV, Forland E, Mietus M, Coelho F, Mares C, Razuvaev V, Nieplova E, Cegnar T, Lopez JA, Dahlström B, Moberg A, Kirchhofer W, Ceylan A, Pachaliuk O, Alexander LV, Petrovic P (2002) Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. International Journal of Climatology 22: 1441-1453

Klomp H (1970) Clutch size in birds. Ardea 58: 1-121

Kluyver HN, Tinbergen L (1953) Territory and the regulation of density in titmice. Archives Néerlandaises de Zoologie 10: 265-289

Koffijberg K, Günther K (2005) Recent population dynamics and habitat use of barnacle geese and dark-bellied brent geese in the Wadden Sea. In: Blew J, Südbeck P (eds) Migratory Waterbirds in the Wadden Sea 1980–2000. Wadden Sea Ecosystem No. 20. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Joint Monitoring Group of Migratory Birds in the Wadden Sea, Wilhelmshaven, Germany,

Kokko H (1999) Competition for early arrival in migratory birds. Journal of Animal Ecology 68: 940-950

Korschgen CE, Kenow KP, Gendron-Fitzpatrick A, Green WL, Dein FJ (1996) Implanting intra-abdominal radiotransmitters with external whip antennas in ducks. Journal of Wildlife Management 60: 132-137

Korte H (1988) Measuring condition in brent geese *Branta b. bernicla*. MSc Thesis, University Groningen

Koskimies J, Lahti L (1964) Cold-hardiness of the newly-hatched young in relation to ecology and distribution in ten species of European ducks. Auk 81: 281-307

Krechmar AV, Kondratyev AV (2006) Waterfowl Birds of North-East Asia. Acad Sci, Far East Branch, Magadan

Kumari E (1971) Passage of the barnacle goose through the Baltic area. Wildfowl 22: 25-43

Kymenlaakso Birding Society (1990-2004) Annual reports published in Lintukymi.

Kvist A, Lindström Å, Green M, Piersma T, Visser GH (2001) Carrying large fuel loads during sustained bird flight is cheaper than expected. Nature 413: 730-732

L

Lack D (1966) Population Studies of Birds. Clarendon, Oxford

Lack D (1968) Ecological Adaptations for Breeding in Birds. Chapman and Hall, London

Lank DB, Butler RW, Ireland J, Ydenberg RC (2003) Effects of predation danger on migration strategies of sandpipers. Oikos 103: 303-319

Larsson K (1996) Genetic and environmental effects on the timing of wing moult in the barnacle goose. Heredity 76: 100-107

Larsson K, Forslund P (1991) Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. Journal of Evolutionary Biology 4: 619-636

Larsson K, Forslund P (1994) Population dynamics of the barnacle goose, *Branta leucopsis*, in

the Baltic area: density-dependent effects on reproduction. Journal of Animal Ecology 63: 954-962
Larsson K, Forslund P, Gustafsson L, Ebbinge BS (1988) From the High Arctic to the Baltic: the successful establishment of a barnacle goose *Branta leucopsis* population on Gotland, Sweden. Ornis Scandinavica 19: 182-189
Larsson K, Tegelström H, Forslund P (1995) Intraspecific nest parasitism and adoption of young in the barnacle goose: effects on survival and reproductive performance. Animal Behaviour 50: 1349-1360
Larsson K, Van der Jeugd HP (1998) Continuing growth of the Baltic barnacle goose population: number of individuals and reproductive success in different colonies. Norsk Polar Institutt Skrifter 200: 213-219
Larsson K, Van der Jeugd HP, Van der Veen IT, Forslund P (1998) Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. Evolution 52: 1169-1184
Le Maho Y, Vu Van Kha H, Koubi H, Dewasmes G, Girard J, Ferre P, Cagnard M (1981) Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. American Journal of Physiology 241: E342-E354
Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67-118
Leito A (1996) The barnacle goose in Estonia. Estonia Maritima 1: 1-103
Leito A, Renno O, Kuresoo A (1991) Spring numbers and distribution of barnacle goose *Branta leucopsis* staging in Estonia. Wildfowl 42: 37-41
Leito A, Truu J (2004) Changes in distribution and numbers of the barnacle goose (*Branta leucopsis*) in Estonia. Estonia Maritima 6: 111-127
Lepage D, Desrochers A, Gauthier G (1999) Seasonal decline of growth and fledging success in snow geese *Anser caerulescens*: an effect of date or parental quality? Journal of Avian Biology 30: 72-78
Lepage D, Gauthier G, Menu S (2000) Reproductive consequences of egg-laying decisions in snow geese. Journal of Animal Ecology 69: 414-427
Lepage D, Gauthier G, Reed A (1998) Seasonal variation in growth of greater snow goose goslings: the role of food supply. Oecologia 114: 226-235
Lessells CM (1986) Brood size in Canada geese: a manipulation experiment. Journal of Animal Ecology 55: 669-690
Lessells CM, Boag PT (1987) Unrepeatable repeatabilities - a common mistake. Auk 104: 116-121
Lessells CM, Sibly RM, Owen M, Ellis S (1979) Weights of female barnacle geese during breeding. Wildfowl 30: 72-74
Lindström Å (2003) Fuel deposition rates in migrating birds: causes, constraints and consequences. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian Migration. Springer-Verlag, Berlin Heidelberg, pp 307-320
Lindström Å, Piersma T (1993) Mass changes in migrating birds - the evidence for fat and protein storage re-examined. Ibis 135: 70-78
Long PR, Székely T, Kershaw M, O'Connell M (2007) Ecological factors and human threats both drive wildfowl population declines. Animal Conservation 10: 183-191
Loonen MJJE, Follestad A (1997) Geographical variation in the timing of wing moult in greylag geese *Anser anser*. In: Loonen MJJE (ed) Goose Breeding Ecology: Overcoming Successive Hurdles to Raise Goslings. PhD Thesis. University of Groningen, Groningen
Loonen MJJE, Larsson K, Van der Veen IT, Forslund P (1997) Timing of wing moult and growth of young in arctic and temperate-breeding barnacle geese. In: Loonen MJJE (ed) Goose Breeding Ecology: Overcoming Successive Hurdles to Raise Goslings. PhD Thesis. University of Groningen, Groningen, pp 136-153
Loudon H, Buturlin SA (1908) Eine ornithologische Fahrt an die Matzal Wiek. Journal für Ornithologie 56: 61-72

M

Madsen J (1985) Relations between change in spring habitat selection and daily energetics of pink-footed geese *Anser brachyrhynchus*. Ornis Scandinavica 16: 222-228

Madsen J (2001) Spring migration strategies in pink-footed geese *Anser brachyrhynchus* and consequences for spring fattening and fecundity. Ardea 89: 43-55

Madsen J, Fox AD, Cracknell J (1999) Goose Populations of the Western Palearctic. Wetlands International, Wageningen

Madsen J, Klaassen M (2006) Assessing body condition and energy budget components by scoring abdominal profiles in free-ranging pink-footed geese *Anser brachyrhynchus*. Journal of Avian Biology 37: 283-287

Mann FE, Sedinger JS (1993) Nutrient-reserve dynamics and control of clutch size in northern pintails breeding in Alaska. Auk 110: 264-278

Martin LB, Pless M, Svoboda J, Wikelski M (2004) Immune activity in temperate and tropical house sparrows: A common-garden experiment. Ecology 85: 2323-2331

Mata AJ, Caloin M, Robin JP, Le Maho Y (2006) Reliability in estimates of body composition of birds: Oxygen-18 versus deuterium dilution. Physiological and Biochemical Zoology 79: 202-209

McCleery RH, Perrins CM (1998) …temperature and egg-laying trends. Nature 391: 30-31

McDonald P, Edwards RA, Greenhalgh JFD, Morgan CA (1995) Animal Nutrition. Longman, United Kingdom

McLandress MR, Raveling DG (1981) Changes in diet and body composition of Canada geese before spring migration. Auk 98: 65-79

McNab BK (2002) The Physiological Ecology of Vertebrates: A View from Energetics. Cornell University Press, Ithaca, New York

McNaughton SJ (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113: 691-703

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124: 863-886

Meijer T, Drent R (1999) Re-examination of the capital and income dichotomy in breeding birds. Ibis 141: 399-414

Meininger PL, Van Swelm ND (1994) Brandganzen *Branta leucopsis* als broedvogel in het Deltagebied. Limosa 67: 1-5

Menu S, Gauthier G, Reed A (2005) Survival of young greater snow geese (*Chen caerulescens atlantica*) during fall migration. Auk 122: 479-496

Merilä J, Kruuk LEB, Sheldon BC (2001) Cryptic evolution in a wild bird population. Nature 412: 76-79

Miller MR (1989) Estimating carcass fat and protein in northern pintails during the nonbreeding season. Journal of Wildlife Management 53: 123-129

Miller MR, Eadie JM (2006) The allometric relationship between resting metabolic rate and body mass in wild waterfowl (*Anatidae*) and an application to estimation of winter habitat requirements. Condor 108: 166-177

Miller MR, Takekawa JY, Fleskes JP, Orthmeyer DL, Casazza ML, Perry WM (2005) Spring migration of northern pintails from California's Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. Canadian Journal of Zoology 83: 1314-1332

Møller AP (2001) Heritability of arrival date in a migratory bird. Proceedings of the Royal Society of London Series B 268: 203-206

Møller AP, Fiedler W, Berthold P (eds) (2004) Birds and climate change. Advances in Ecological Research 35: 1-251

Monaghan P, Nager RG (1997) Why don't birds lay more eggs? Trends in Ecology & Evolution 12: 270-274

Moore F, Mabey S, Woodrey M (2003) Priority access to food in migratory birds: age, sex and motivational asymmetries. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian Migration. Springer-Verlag, Berlin Heidelberg, pp 281-292

Moreno J (1989) Strategies of mass change in breeding birds. Biological Journal of the Linnean Society 37: 297-310
Morozov VV (2001) Faunistic material on birds of Vaygach Island. Ornitologiya 29: 29-46
Morrison RIG (2006) Body transformations, condition, and survival in red knot *Calidris canutus* travelling to breed at Alert, Ellesmere Island, Canada. Ardea 94
N
Nager RG (2006) The challenges of making eggs. Ardea 94: 323-346
Nager RG, Keller LF, Van Noordwijk AJ (2000) Understanding natural selection on traits that are influenced by environmental conditions. In: Mousseau TA, Sinervo B, Endler JA (eds) Adaptive Genetic Variation in the Wild. Oxford University Press, Oxford, pp 95-115
Newton I (1977) Timing and success of breeding in tundra-nesting geese. In: Stonehouse B, Perrins C (eds) Evolutionary Ecology. Macmillan, London, pp 113-126
Newton I (2006) Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147: 146-166
Newton I (2007) Weather-related mass-mortality events in migrants. Ibis 149: 453-467
Nolet BA (2006) Speed of spring migration of tundra swans *Cygnus columbianus* in accordance with income or capital breeding strategy? Ardea 94: 579-591
Nolet BA, Butler PJ, Masman D, Woakes AJ (1992) Estimation of daily energy expenditure from heart rate and doubly labeled water in exercising geese. Physiological Zoology 65: 1188-1216
Nolet BA, Drent RH (1998) Bewick's swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. Journal of Avian Biology 29: 574-581
Nolet BA, Klaassen M (2005) Time and energy constraints in demanding phases of the annual cycle: an example of time limitation in refuelling migratory swans. Oikos 111: 302-310
Nowak E (1995) Jagdaktivitäten in der Vergangenheit und heute als Einflußfaktor auf Gänsepopulationen und andere Vögel Nordsibiriens. In: Prokosch P, Hötker H (eds) Faunistik und Naturschutz auf Taimyr - Expeditionen 1989-1991. Corax (spec. issue)16: 143-159
Nur N (1990) The consequences of brood size for breeding blue tits III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. Evolution 42: 351-362
O
Odum EP, Rogers DT, Hicks DL (1964) Homeostasis of the nonfat components of migrating birds. Science 143: 1037-1039
Ogilvie M (1978) Wild Geese. Poyser, Berkhamsted
Olsen J, Seierstad I, Vinther B, Johnsen S, Heinemeier J (2006) Memory effect in deuterium analysis by continuous flow isotope ratio measurement. International Journal of Mass Spectrometry 254: 44-52
Ouweneel GL (2001) Snelle groei van de broedpopulatie Brandganzen *Branta leucopsis* in het deltagebied. Limosa 74: 137-146
Owen M (1980) Wild Geese of the World: Their Life History and Ecology. Batsford Ltd, London
Owen M, Black JM (1989) Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58: 603-617
P
Pace N, Rathbun EN (1945) Studies on body composition. III. The body water and chemically combined nitrogen content in relation to fat content. Journal of Biological Chemistry 158: 685-691
Parker H, Holm H (1990) Patterns of nutrient and energy expenditure in female common eiders nesting in the High Arctic. Auk 107: 660-668
Paxinos EE, James HF, Olson SL, Sorenson MD, Jackson J, Fleischer RC (2001) mtDNA from fossils reveals a radiation of Hawaiian geese recently derived from the Canada goose (*Branta canadensis*). Proceedings of the National Academy of Sciences of the USA 99: 1399-1404

Pennycuick CJ (1975) Mechanics of flight. In: Farner DS, King JR (eds) Avian Biology. Academic Press, London, pp 1-75
Percival SM, Percival T (1997) Feeding ecology of barnacle geese on their spring staging grounds in northern Iceland. Ecography 20: 461-465
Perrins CM (1970) The timing of birds' breeding season. Ibis 112: 242-255
Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. Oecologia 127: 171-179
Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Bennett VJ (2005) Summer distribution and migration of nonbreeding albatrosses: Individual consistencies and implications for conservation. Ecology 86: 2386-2396
Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. Marine Ecology Progress Series 266: 265-272
Piersma T (1984) Estimating energy reserves of great crested grebes *Podiceps cristatus* on the basis of body dimensions. Ardea 72: 119-126
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
Piersma T, Lindström Å, Drent RH, Tulp I, Jukema J, Morrison RIG, Reneerkens J, Schekkerman H, Visser GH (2003) High daily energy expenditure of incubating shorebirds on High Arctic tundra: a circumpolar study. Functional Ecology 17: 356-362
Pistorius PA, Follestad A, Taylor FE (2006) Temporal changes in spring migration phenology in the Norwegian greylag goose *Anser anser*, 1971-2004. Wildfowl 56: 23-36
Ploeger PL (1968) Geographical differentiation in arctic Anatidae as a result of isolation during last glacial. Ardea 56: 1-159
Podlesak DW, McWilliams SR, Hatch KA (2005) Stable isotopes in breath, blood, feces and feathers can indicate intra-individual changes in the diet of migratory songbirds. Oecologia 142: 501-510
Poisbleau M, Dalloyau S, Fritz H, Bost CA, Ebbinge BS (2007) Brent goose *Branta bernicla bernicla* feeding behaviour during incubation, Taimyr Peninsula, Russia. Polar Biology 30: 1343-1349
Pokrovskaya LV, Gavrilo MV (1998) Present distribution of barnacle goose in Russia. Problems of conservation of poorly studied fauna of the North. Materials for the Red Data Book. Moscow, pp 92-100
Ponomareva TS (1992) Barnacle goose nesting in the Kolguyev Island region. Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii 98: 39-44
Popov AA (1937) Okhota i rybolovstvo u Dolgan. Pamyati V.G. Bogoraza 1865-1936. Akademii nauk, Moscow, pp 147-206
Poussart C, Gauthier G, Larochelle J (2001) Incubation behaviour of greater snow geese in relation to weather conditions. Canadian Journal of Zoology 79: 671-678
Pouw A, Van der Jeugd HP, Eichhorn G (2005) Broedbiologie van Brandganzen *Branta leucopsis* op de Hellegatsplaten. Student report, Groningen
Price T, Liou L (1989) Selection on clutch size in birds. American Naturalist 134: 950-959
Prins HHT, Ydenberg RC (1985) Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). Oecologia 66: 122-125
Prop J (2004) Food Finding: On the Trail to Successful Reproduction in Migratory Geese. PhD Thesis. University of Groningen, Groningen
Prop J, Black JM (1998) Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. Norsk Polarinstitutt Skrifter 200: 175-193
Prop J, Black JM, Shimmings P (2003) Travel schedules to the High arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. Oikos 103: 403-414
Prop J, de Vries J (1993) Impact of snow and food conditions on the reproductive performance of barnacle geese *Branta leucopsis*. Ornis Scandinavica 24: 110-121
Prop J, Deerenberg C (1991) Spring staging in brent geese *Branta bernicla*: feeding

constraints and the impact of diet on the accumulation of body reserves. Oecologia 87: 19-28

Prop J, Spaans B (2004) Body stores in pre-migratory brent geese: the consequence of habitat choice on protein deposition. In: Prop J (ed) Food finding: On the Trail to Successful Reproduction in Migratory Geese. PhD thesis. University of Groningen, Groningen, pp 71-85

Prop J, Van Eerden MR, Drent RH (1984) Reproductive success of the barnacle goose in relation to food exploitation on the breeding grounds, western Spitsbergen. Norsk Polarinstitutt Skrifter 181: 87-117

Prop J, Vulink T (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Functional Ecology 6: 180-189

Pulido F, Berthold P, Mohr G, Querner U (2001) Heritability of the timing of autumn migration in a natural bird population. Proceedings of the Royal Society of London Series B 268: 953-959

R

Randla T (1976) Estonian Birds of Prey. Tallinn

Rasbash J, Steele F, Browne W, Prosser B (2004) A user's guide to MLwiN - version 2.0. Centre for Multilevel Modeling, London

Raveling DG (1979) The annual cycle of body composition of Canada geese with special reference to control of reproduction. Auk 96: 234-252

Reed A, Hughes RJ, Gauthier G (1995) Incubation behavior and body mass of female greater snow geese. Condor 97: 993-1001

Rees EC (1989) Consistency in the timing of migration for individual Bewick's swans. Animal Behaviour 38: 384-393

Reese EC (2006) Bewick's Swan. T & AD Poyser, London

Reinecke KJ, Stone TL, Owen RB (1982) Seasonal carcass composition and energy balance of female black ducks in Maine. Condor 84: 420-426

Ricklefs RE (1980) Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97: 38-49

Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. Trends in Ecology & Evolution 17: 462-468

Rohwer FC (1992) The evolution of reproductive patterns in waterfowl. In: Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) Eology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, pp 486-539

Rohwer FC, Anderson MG (1988) Female-biased philopatry, monogamy, the timing of pair formation in waterfowl. In: Johnston RF (ed) Current Ornithology. Plenum Press, New York, pp 187-221

Ryder JP (1970) A possible factor in evolution of clutch size in Ross goose. Wilson Bulletin 82: 5-13

S

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, Van Bommel FPJ (2006) Long-term population declines in Afro-Palearctic migrant birds. Biological Conservation 131: 93-105

Schmutz JA, Hobson KA, Morse JA (2006) An isotopic assessment of protein from diet and endogenous stores: effects on egg production and incubation behaviour of geese. Ardea 94: 385-397

Schoeller DA, Van Santen E, Peterson DW, Dietz W, Jaspan J, Klein PD (1980) Total body water measurement in humans with ^{18}O and ^{2}H labeled water. American Journal of Clinical Nutrition 33: 2686-2693

Schubert CA, Cooke F (1993) Egg-laying intervals in the lesser snow goose. The Wilson Bulletin 105: 414-426

Schwilch R, Piersma T, Holmgren NMA, Jenni L (2002) Do migratory birds need a nap after a long non-stop flight? Ardea 90: 149-154

Seber GAF (1982) The Estimation of Animal Abundance and Related Parameters. Griffin, London

Sedinger JS (1984) Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. Journal of Wildlife Management 48: 1128-1136
Sedinger JS, Flint PL (1991) Growth-rate is negatively correlated with hatch date in black brant. Ecology 72: 496-502
Sedinger JS, Raveling DG (1986) Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. Journal of Animal Ecology 55: 1083-1102
Sedinger JS, Raveling DG (1988) Foraging behavior of cackling Canada goose goslings: implications for the roles of food availability and processing rate. Oecologia 75: 119-124
Sedinger JS, White RG, Hauer WE (1992) Heat increment of feeding and partitioning of dietary energy in yearling black brant. Canadian Journal of Zoology 70: 1047-1051
Shaffer SA, Gabrielsen GW, Verreault J, Costa DP (2006) Validation of water flux and body composition in glaucous gulls (*Larus hyperboreus*). Physiological and Biochemical Zoology 79: 836-845
Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71: 296-308
Skagen SK, Knopf FL, Cade BS (1993) Estimation of lipids and lean mass of migrating sandpipers. Condor 95: 944-956
Skalski JR, Hoffmann A, Smith SG (1993) Testing the significance of individual- and cohort-level covariates in animal survival studies. In: Lebreton JD, North PM (eds) Marked Individuals in the Study of Bird Populations. Birkhäuser Verlag, Basel, pp 9-28
Smith RJ, Moore FR (2003) Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia 134: 325-331
Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening dark-bellied brent geese *Branta bernicla*. Ardea 89: 427-440
Spaans B, Van der Veer W, Ebbinge BS (1999) Cost of incubation in a greater white-fronted Goose. Waterbirds 22: 151-155
Spaans B, Van't Hoff CA, Van der Veer W, Ebbinge BS (2007) The significance of female body stores for egg laying and incubation in dark-bellied brent geese *Branta bernicla bernicla*. Ardea 95: 3-15
Speakman JR (ed) (2001) Body Composition Analysis of Animals: A Handbook of Non-Destructive methods. Cambridge University Press, Cambridge
Speakman JR, Visser GH, Ward S, Krol E (2001) The isotope dilution method for the evaluation of body composition. In: Speakman JR (ed) Body Composition Analysis of Animals: A Handbook of Non-Destructive Methods. Cambridge University Press, Cambridge, pp 56-98
Stahl J (2001) Limits to the Co-Occurence of Avian Herbivores - How Geese Share Scarce Resources. PhD thesis. University of Groningen, Groningen
Stahl J, Van der Graaf AJ, Drent RH, Bakker JP (2006) Subtle interplay of competition and facilitation among small herbivores in coastal grasslands. Functional Ecology 20: 908-915
Stahl J, Veeneklaas RM, Van der Graaf AJ, Loonen MJJE, Drent RH (2001) Conversion factors for energetic expenditure of actively foraging brent and barnacle geese obtained by non-invasive heart rate telemetry. In: Stahl J (ed) Limits to the Co-Occurence of Avian Herbivores - How Geese Share Scarce Resources. PhD thesis. University of Groningen, Groningen
Stearns SC (1992) The Evolution of Life Histories. Oxford University Press, New York
Stervander M, Lindström Å, Jonzén N, Andersson A (2005) Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. Journal of Avian Biology 36: 210-221
Stevenson RD, Woods WA (2006) Condition indices for conservation: new uses for evolving tools. Integrative and Comparative Biology 46: 1169-1190
Stewart GR, Lee JA (1974) The role of proline accumulation in halophytes. Planta 120: 279-289

Stock M, Hofeditz F (2002) Einfluss des Salzwiesen-Managements auf Habitatnutzung und Bestandsentwicklung von Nonnengänsen *Branta leucopsis* im Wattenmeer. Vogelwelt 123: 265-282

Sutherland WJ (1998) Evidence for flexibility and constraint in migration systems. Journal of Avian Biology 29: 441-446

Swennen C, Ursem JCH, Duiven P (1993) Determinate laying and egg attendance in common eiders. Ornis Scandinavica 24: 48-52

Syroechkovsky Jr. EE (1995) News in distribution of barnacle boose in Russia. Casarca 1: 39-46

T

Takekawa JY, Kurechi M, Orthmeyer DL, Sabano Y, Uemura S, Perry WM, Yee JL (2000) A Pacific spring migration route and breeding range expansion for greater white-fronted geese wintering in Japan. Global Environmental Research 4: 155-168

Terpstra K, De Hart N (1974) The estimation of urinary nitrogen and fecal nitrogen in poultry excreta. Zeitschrift für Tierphysiologie, Tierernährung und Futtermittelkunde 32: 306-320

Thomas VG, Mainguy SK, Prevett JP (1983) Predicting fat content of geese from abdominal fat weight. Journal of Wildlife Management 47: 1115-1119

Thompson SC, Raveling DG (1987) Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. Auk 104: 707-716

Tieleman BI, Williams JB, Ricklefs RE, Klasing KC (2005) Constitutive innate immunity is a component of the pace-of-life syndrome in tropical birds. Proceedings of the Royal Society of London Series B 272: 1715-1720

Tinbergen JM, Williams JB (2002) Energetics of incubation. In: Deeming DC (ed) Avian Incubation: Behaviour, Environment and Evolution. Oxford University Press, Oxford, pp 299-313

Tombre IM, Erikstad KE (1996) An experimental study of incubation effort in high-Arctic barnacle geese. Journal of Animal Ecology 65: 325-331

Tombre IM, Madsen J, Tømmervik H, Haugen KP, Eythórsson E (2005) Influence of organised scaring on distribution and habitat choice of geese on pastures in Northern Norway. Agriculture, Ecosystems and Environment 111: 311-320

Trevor-Battye A (1895) Ice-bound on Kolguyev. Westminster

V

Van der Graaf AJ (2006) Geese on a Green wave: Flexible Migrants in a Changing World. PhD thesis. University of Groningen, Groningen

Van der Graaf AJ, Bos D, Loonen MJJE, Engelmoer M, Drent RH (2002) Short- and long-term facilitation of goose grazing by livestock. Journal of Coastal Conservation 8: 179-188

Van der Graaf AJ, Feige N, Van der Jeugd HP, Leito A, Larsson K, Litvin KE, Drent RH, Bakker JP, Stahl J (2006a) Has the recent breeding range expansion of Arctic geese been facilitated by changes in human land use? In: Van der Graaf AJ (ed) Geese on a Green wave: Flexible Migrants in a Changing World. PhD thesis. University of Groningen, Groningen

Van der Graaf AJ, Lavrinenko OV, Elsakov V, Van Eerden MR, Stahl J (2004) Habitat use of barnacle geese at a subarctic salt marsh in the Kolokolkova Bay, Russia. Polar Biology 27: 651-660

Van der Graaf AJ, Stahl J, Bakker JP (2005) Compensatory growth of *Festuca rubra* after grazing: can migratory herbivores increase their own harvest during staging? Functional Ecology 19: 961-969

Van der Graaf AJ, Stahl J, Bos D, Drent RH (2001) Influence of wind exposure and temperature on energy expenditure and site choice in brent and barnacle geese. In: Stahl J (ed) Limits to the Co-Occurence of Avian Herbivores - How Geese Share Scarce Resources. PhD thesis. University of Groningen, Groningen

Van der Graaf AJ, Stahl J, Klimkowska A, Bakker JP, Drent RH (2006b) Surfing on a green wave - how plant growth drives spring migration in the barnacle goose *Branta leucopsis*. Ardea 94: 567-577

Van der Graaf AJ, Stahl J, Veeneklaas R, Bakker JP (2007a) The salt marsh of Grötlingboudd, a stopover site for migrating barnacle geese. Annales Botanici Fennici 44: 41

Van der Graaf AJ, Stahl J, Veen GF, Havinga RM, Drent RH (2007b) Patch choice of avian herbivores along a migration trajectory - From Temperate to Arctic. Basic and Applied Ecology 8: 354-363

Van der Jeugd HP (1999) Life History Decisions in a Changing Environment: A Long-term Study of a Temperate Barnacle Goose Population. PhD thesis. University of Uppsala, Uppsala

Van der Jeugd HP, Arisz J, Schouten M (2006) Broedbiologie van brandganzen op de Hellegatsplaten in 2005 en verspreiding buiten het broedseizoen. Unpublished report, Groningen

Van der Jeugd HP, Blaakmeer KB (2001) Teenage love: the importance of trial liaisons, subadult plumage and early pairing in barnacle geese. Animal Behaviour 62: 1075-1083

Van der Jeugd HP, Gurtovaya E, Eichhorn G, Litvin KY, Mineev OY, Van Eerden MR (2003) Breeding barnacle geese in Kolokolkova Bay, Russia: number of breeding pairs, reproductive success and morphology. Polar Biology 26: 700-706

Van der Jeugd HP, Larsson K (1998) Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. Journal of Animal Ecology 67: 953-966

Van der Jeugd HP, Litvin KY (2006) Travels and traditions: long distance dispersal in the barnacle goose exemplified by individual case histories. Ardea 94: 421-432

Van der Jeugd HP, Olthoff MP, Stahl J (2001) Breeding range translates into staging site choice: Baltic and arctic barnacle geese *Branta leucopsis* use different habitats at a Dutch Wadden Sea island. Ardea 89: 253-265

Van der Jeugd HP, Van der Veen IT, Larsson K (2002) Kin clustering in barnacle geese: familiarity or phenotype matching? Behavioral Ecology 13: 786-790

Van der Meer J, Piersma T (1994) Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. Physiological Zoology 67: 305-329

Van der Meijden R (1996) Heukels' Flora van Nederland. Wolters-Noordhoff, Groningen

Van der Wal R, Van de Koppel J, Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: an experiment with barnacle geese. Oikos 82: 123-130

Van Dinteren G (1988) De benutting van de Oosterkweldervegetatie op Schiermonnikoog door de brandgans (*Branta leucopsis*). MSc thesis. University of Groningen, Groningen

Van Eerden MR, Drent RH, Stahl J, Bakker JP (2005) Connecting seas: western Palaearctic continental flyway for water birds in the perspective of changing land use and climate. Global Change Biology 11: 894-908

Van Eerden MR, Zijlstra M, Van Roomen M, Timmerman A (1996) The response of *Anatidae* to changes in agricultural practice: long-term shifts in the carrying capacity of wintering waterfowl. Gibier Faune Sauvage 13: 706

Van Noordwijk AJ, Pulido F, Helm B, Coppack T, Delingat J, Hedenström A., Van der Jeugd HP, Pérez-Tris J (2006) A framework for the study of genetic variation in migratory behaviour. Journal of Ornithology 147: 221-233

Verhulst S, Van Balen JH, Tinbergen JM (1995) Seasonal decline in reproductive success of the great tit - variation in time or quality? Ecology 76: 2392-2403

Vézina F, Williams TD (2003) Plasticity in body composition in breeding birds: What drives the metabolic costs of egg production? Physiological and Biochemical Zoology 76: 716-730

Vézina F, Williams TD (2005) Interaction between organ mass and citrate synthase activity as an indicator of tissue maximal oxidative capacity in breeding European starlings: implications for metabolic rate and organ mass relationships. Functional Ecology 19: 119-128

Vickery JA, Gill JA (1999) Managing grassland for wild geese in Britain: a review. Biological Conservation 89: 93-106

Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society of London Series B 275: 649-659

Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. Proceedings of the Royal Society of London Series B 268: 289-294

Visser ME, Van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society of London Series B 265: 1867-1870

Voslamber B, Van der Jeugd HP, Koffijberg K (2007) Numbers, trends and distribution of breeding goose populations in the Netherlands. Limosa 80: 1-17

Vulink T (2001) Hungry Herds: Management of temperate lowland wetlands by grazing. PhD Thesis. University of Groningen, Groningen; Van Zee tot Land 66, Ministerie van Verkeer en Waterstaat, Directoraat-Generaal Rijkswaterstaat, Directie Ijsselmeergebied

W

Wang ZM, Deurenberg P, Pietrobelli A, Baumgartner RN, Heymsfield SB (1999) Hydration of fat-free body mass: review and critique of a classic body-composition constant. American Journal of Clinical Nutrition 69: 833-841

Ward DH, Reed A, Sedinger JS, Black JM, Derksen DV, Castelli PM (2005) North American brant: effects of changes in habitat and climate on population dynamics. Global Change Biology 11: 869-880

Weber TP, Ens BJ, Houston AI (1998) Optimal avian migration: A dynamic model of fuel stores and site use. Evolutionary Ecology 12: 377-401

White GC, Burnham KP (1999) Program mark: survival estimation from populations of marked animals. Bird Study 46 (suppl.): 120-139

Wiersma P, Munoz-Garcia A, Walker A, Williams JB (2007) Tropical birds have a slow pace of life. Proceedings of the National Academy of Sciences of the USA 104: 9340-9345

Wiersma P, Piersma T (1994) Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. Condor 96: 257-279

Wikelski M, Spinney L, Schelsky W, Scheuerlein A, Gwinner E (2003) Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. Proceedings of the Royal Society of London Series B 270: 2383-2388

Wilson RP, Ducamp JJ, Rees G, Culik BM, Niekamp K (1992) Estimation of location: global coverage using light intensity. In: Priede IM, Swift SM (eds) Wildlife Telemetry: Remote Monitoring and Tracking of Animals. Ellis Horward, Chichester, pp 131-134

Z

Zar JH (1999) Biostatistical Analysis. Prentice Hall, Upper Saddle River, New Jersey

Samenvatting

Management van tijd en energie
Alle levensprocessen vereisen energie en voedingstoffen (in de tekst verder ook 'resources' of 'bronnen' genoemd). De efficiëntie waarmee organismen deze fundamentele bronnen kunnen benutten heeft directe consequenties voor hun 'fitness' (dus op de overleving en het voortplantingssucces van het individu). De mate waarin een individu deze bronnen nodig heeft, varieert gedurende de jaarlijkse cyclus. Het voortplantingsseizoen neemt hierbij een belangrijke plaats in, omdat in deze periode volwassen dieren niet alleen voedsel moeten vinden voor zichzelf, maar ook voor hun jongen. Beschikbaarheid van deze bronnen is gedurende het seizoen in de meeste gebieden aan grote schommelingen onderhevig. Er is dus een sterke selectiedruk om de snel wisselende vraag naar bronnen precies af te stemmen op de beschikbaarheid van deze bronnen. Kortom, het maximeren van de fitness betekent vooral een zo optimaal mogelijke management van tijd en energie.

Voor- en nadelen van vogeltrek
De mogelijkheid tot vliegen geeft vogels de mogelijkheid om voedselbronnen verspreid over een groot gebied te benutten. Vogels die trekken kunnen gebruik maken van een verschuivende piek in voedselaanbod langs een klimatologische gradiënt. Zo kunnen in de Arctis broedende ganzen tijdens hun voorjaarstrek profiteren van een soort 'groene golf' van plantengroei waarbij ze op opeenvolgende pleisterplaatsen langs de trekroute gebruik kunnen maken van voedsel met steeds een hoge kwaliteit (mals, goed verteerbaar gras in de voorjaarsgroei). Goede voedselomstandigheden zijn belangrijk voor een snelle opbouw van lichaamsreserves. Door voedingsstoffen op te slaan (met name vetten en eiwitten) en mee te nemen naar de broedgebieden, kunnen ze uiteindelijk de golf van voedselpieken voorblijven. Dit maakt hen minder afhankelijk van de voedselsituatie ter plekke waardoor ze vroeg in het seizoen kunnen beginnen met broeden wanneer nog weinig voedsel beschikbaar is. Vroeg beginnen met broeden is een voorwaarde om de kuikenfase te kunnen afstemmen op de periode wanneer het voedselaanbod maximaal is.

Echter, elk voordeel heeft zijn nadeel. De periode van trek vergt extra tijd en energie, waarmee het juiste management van deze bronnen nog belangrijker wordt. Door mogelijke gevaren en onheil tijdens de trek (uitputting, predatie, slechte weersomstandigheden), zou de trek een hoge tol kunnen eisen in vergelijking met andere fasen van de jaarlijkse cyclus. En tenslotte, veel trekvogels zijn afhankelijk van vele en zeer specifieke pleisterplaatsen ('stop over sites') om bij te tanken. Hierdoor zijn ze ook kwetsbaarder voor een verslechterde situatie of voor verstoring op deze cruciale pleisterplaatsen.

Flexibiliteit en beperkingen in de trek- en broedbiologie van de brandgans
Dit proefschrift onderzoekt de aspecten van de tijdsplanning en het verkrijgen en benutten van voedselbronnen in de brandgans *Branta leucopsis* tijdens de voorjaarstrek en tijdens het broedseizoen. De bestudeerde brandganspopulatie overwintert in het Waddenzeegebied, en trekt traditioneel via pleisterplaatsen langs de Oostzee (Gotland, Öland, Estland) en de Witte Zee naar Arctisch-Russische broedgebieden aan de Barentszzee (Nova Zembla, Vajgatsj, Petsjora Delta). Deze populatie heeft de afgelopen decennia enige opmerkelijke ontwikkelingen doorgemaakt.

Ten eerste, nadat de populatie tot een dieptepunt van 20000 vogels in de jaren '50 was gezakt, is de populatie sindsdien exponentieel gegroeid naar meer dan een half miljoen exemplaren heden ten dage. Ten tweede, sinds de vroege jaren '90 vertrekt een steeds groter deel van de populatie steeds later uit de wintergebieden in de Waddenzee. In de laatste jaren wordt het vertrek zelfs met vier weken uitgesteld. Ten derde, de soort werd lange tijd beschouwd als een typische Arctische broedvogel, maar de afgelopen drie decennia koloniseert de soort met succes een grote diversiteit van gebieden in de gematigde zone. Daarmee hebben deze vogels de afstand tot de broedgebieden (voorheen ca. 3500 km) flink ingekort, en sommige ganzenpopulaties vertonen nu helemaal geen trek meer. De uitbreiding van het verspreidingsgebied lijkt in tegenspraak met de noordwaartse verschuiving die men zou kunnen verwachten als gevolg van de klimaatsverandering. Deze opmerkelijke veranderingen werpen vragen op betreffende de flexibiliteit van trekschema's en broedcycli. Wat zijn de kosten en baten van verschillende trekstrategieën? Tot op welke hoogte zijn de dieren in staat zich aan te passen aan nieuwe (broed-) omgevingen?

Hoewel men tegenwoordig beseft dat migratie en reproductie nauw met elkaar verweven zijn, wordt het volgen van individuen tijdens de vogeltrek over lange afstanden nog nauwelijks gekoppeld aan gegevens over de broedbiologie. Dit proefschrift probeert deze lacune in kennis op te vullen voor de brandganspopulatie die in het Arctische gebied van Rusland broedt. Het andere centrale thema in dit proefschrift is de vergelijking binnen de soort van belangrijke kenmerken van levensgeschiedenis ("life-history traits"; zoals overleving en legselgrootte) van broedpopulaties langs een grote ecologische gradiënt van de Arctis (Barentszzee) tot gematigde zones (Oost- en Noordzee). We verwachten dat elk gebied door verschillen in ecologische parameters een andere selectiedruk uitoefent op de broedpopulatie.

Zoals in de meeste studies, ligt de nadruk op de geslachtsrijpe volwassen brandganzenvrouwtjes. Ten eerste, omdat zij de belangrijkste rol spelen in het tijd- en

resourcemanagement (vooral van lichaamsreserves) voor reproductie. Ten tweede, omdat het bij ganzen gebruikelijk is dat vooral de vrouwtjes de uiteindelijke broedplekken uitzoeken.

Naast een inleidend hoofdstuk (hoofdstuk 1), is dit proefschrift opgedeeld in drie delen en wordt het afgesloten met algemene discussie van de onderzoeksresultaten en perspectieven voor verder onderzoek (hoofdstuk 8).

Deel 1: Onderzoeksmateriaal en –technieken
Dit deel beschrijft de belangrijkste technieken die we gebruikten enerzijds om individuele ganzen te volgen in tijd en ruimte, en anderzijds na te gaan hoe ganzen hun lichaamsreserves opbouwen en gebruiken. **Box A** gaat over twee technieken die we gebruikten om de individuele trekbewegingen van brandganzen in kaart te brengen. Deze technieken zijn: satelliettelemetrie door middel van geïmplanteerde zenders en Global Location Sensing (GLS) (positiebepaling op basis van tijd- en lichtmetingen) met op de pootringen aangebrachte dataloggers. Tijdens de duur van de studie (2 tot 3 jaar vanaf het moment dat de instrumenten waren aangebracht) vonden we geen nadelige effecten van de zenders en dataloggers op de overleving van de ganzen. Verder bleek het tijdsverloop van de trek en het broeden van vogels met en zonder deze instrumenten zeer vergelijkbaar (hoofdstuk 3 en 4). Daarom hebben we een groot vertrouwen dat de verzamelde gegevens representatief zijn voor de ganzen van onze studiegebieden. Naast 'remote tracking' technieken, werd er ook een groot ringprogramma opgezet, dat alle drie de studiepopulaties (Barentsz-, Oost-, en Noordzee) betrof. Daarmee waren visuele waarnemingen van deze geringde dieren in de broed- en overwinteringgebieden mogelijk die ons belangrijke informatie gaven over bijvoorbeeld overlevingskansen (hoofdstuk 6).

In **Hoofdstuk 2** kalibreren en evalueren we een isotopen-verdunnings-methode (met een karkasanalyse als standaard) om bij brandganzen in het veld op niet-destructieve wijze de lichaamssamenstelling te bepalen (hoofdstuk 7 en Box D). Daarvoor wordt een oplossing van met isotopen gemarkeerde watermoleculen (deuterium in dit geval) geïnjecteerd in het dier. Na enige tijd, wanneer deze oplossing voldoende gemengd is met het lichaamsvocht, wordt een bloedmonster genomen en wordt het gehalte aan gemarkeerde moleculen in het bloed bepaald. Met dit gehalte kan de hoeveelheid lichaamswater worden berekend. Met een bekend gehalte aan lichaamswater, het watergehalte in vetvrij lichaamsgewicht en het lichaamsgewicht kan dan een schatting van vet en vetvrij lichaamsgewicht worden gemaakt. Vervolgens verschaft **Box B** aanvullende gegevens over de samenstelling (vet- en watergehaltes) van het karkas op orgaanniveau. Het watergehalte dat gemeten werd in vetvrij spierweefsel, kwam later van pas bij het omrekenen van eiwitreserves tussen vers- en drooggewicht (hoofdstuk 7, Box D).

Deel II: Trekken om te broeden
In 2004 hebben we de eerste gegevens omtrent de trekbewegingen van vrouwtjes van de Russische broedkolonie verkregen met behulp van GLS dataloggers. Deze

gegevens zijn beschreven in **hoofdstuk 3**. De meeste van onze vogels bleken een nieuwe strategie te volgen: zij stelden hun vertrek uit de wintergebieden aanzienlijk uit (tot wel 4 weken) in tegenstelling tot het massale vertrek in vroegere tijden. Door het late vertrek uit de Waddenzee, was de tijd die zij in de Baltische staten doorbrachten ingekort of sloegen zij de pleisterplaatsen in de Oostzee, die in het verleden normaal gesproken door de gehele populatie aangedaan werd, vrijwel geheel over. Het vertrek uit de Oostzee was min of meer gelijktijdig aan het massale vertrek in vroegere jaren. Ongeacht of er wel gebruik gemaakt werd van de Baltische pleisterplaatsen (traditionele strategie) of niet (nieuwe strategie), bleken alle vogels een min of meer vergelijkbare tijdsperiode van ongeveer drie weken op de Arctische pleisterplaatsen (vooral aan de Dvina rivier en op schiereiland Kanin) door te brengen.

In **hoofdstuk 4** onderzoeken we de veranderingen in trekbewegingen meer in detail, waarbij we gebruik maken van lange-termijn gegevens van de voorjaarstrek op drie locaties langs de route (Waddenzee, Zweden en Finland) evenals populatietellingen en temperatuurgegevens. De gegevens van de GLS-dataloggers en satellietzenders van twee jaren (2004-05) maakten het mogelijk de variabiliteit tussen en binnen individuen te bepalen van voorjaarstrekbewegingen in verschillende jaren. Bovendien konden we onderzoeken of een verschil in trekstrategie een verschil in de planning van het broedseizoen veroorzaakt. Wij vinden een enorme flexibiliteit in de planning van de ganzentrek. Het tijdstip van vertrek uit de wintergebieden blijkt wel acht weken uit elkaar te kunnen liggen voor individuen uit dezelfde Arctische broedkolonie. Eén individu wisselde zelfs van de traditionele naar de nieuwe strategie (minder tijd werd doorgebracht op de pleisterplaats in de Oostzee ten gunste van een langer verblijf in de Waddenzee), waarbij het in het tweede jaar 45 dagen later bleek te vertrekken dan het jaar tevoren. Wij veronderstellen dat de nieuwe trekstrategie ontstaan is als gevolg van toenemende competitie voor voedsel op de pleisterplaatsen in de Oostzee. Volgens een analytisch rekenmodel gebaseerd op de optimale migratie theorie kan worden verwacht dat de ganzen de nieuwe strategie zullen overnemen zodra de 'opvetsnelheid' ('fuel deposition rate') in de Oostzee in vergelijking met de Waddenzee onder 88% daalt. We hebben tot dusverre nog geen nadelige effecten kunnen aantonen op voortplantingskansen bij ganzen met de nieuwe strategie. Het tijdstip van eileg (een parameter met veel invloed op het broedsucces) was onafhankelijk van de datum van vertrek uit de Waddenzee. Daarnaast neemt het aandeel ganzen dat laat vertrekt uit de Waddenzee over de laatste 15 jaar alleen maar toe, terwijl de Russische brandganspopulatie een ononderbroken geometrische groei laat zien. Klaarblijkelijk zijn ganzen in staat zich door aanpassingen in habitat- en voedselgebruik optimaal te verdelen over alle voedselbronnen in het gehele Oost-Noordzeegebied. Op deze wijze ontlopen ze mogelijk het probleem dat door de toegenomen voedselcompetitie op de pleisterplaatsen in het Oostzeegebied het voedselaanbod ontoereikend zou zijn.

Hoofdstuk 5 geeft een overzicht hoe belangrijk de lente pleisterplaatsen zijn voor het broedsucces van de ganzen die in het Arctische gebied broeden. Wij benadrukken de noodzaak van voldoende lichaamsreserves voor incubatie, die de (extra)

behoefte die nodig is om alleen maar eieren te maken ver overstijgt. Aan deze totale behoefte kan niet worden voldaan als alleen maar op de broedgebieden gefoerageerd wordt en deze moet voor een belangrijk deel aangevuld worden door lichaamsreserves die opgebouwd zijn op de pleisterplaatsen die bezocht worden vóór het broedseizoen.

Deel III: Waarom zou je trekken om te broeden: een noord-zuid vergelijking
In dit deel vergelijken we drie brandgans broedpopulaties langs de Russische-Baltische trekbaan; één Arctische populatie (Barentszzee), en twee populaties van de gematigde zone (Oostzee en Noordzee). In **hoofdstuk 6** richten we ons met name op de vergelijking van de timing van broeden en het voortplantingssucces. De brandganzen in de Noord- en Oostzee beginnen 6 tot 7 weken eerder met het broeden dan hun soortgenoten aan de Barentszzee. We laten zien hoe het tijdstip van broeden in de Arctische populatie samenvalt met de periode waarin het maximale aantal jongen grootgebracht wordt, terwijl juist de populaties in gematigde streken te laat leggen om een maximaal voortplantingssucces te halen. De zuidelijke broedvogels lijken aan hun nieuwe omgeving nog niet volledig aangepast te zijn of lopen tegen grenzen aan die een optimale aanpassing onmogelijk maken. Echter, de overlevingskans van de jongen tot het tijdstip dat ze de wintergebieden bereiken is veel lager voor de Arctische populatie, wat wijst op de risico's van de trek.

De tijd dat de eieren uitgebroed worden is een periode van grote voedselstress voor het vrouwtje. Ze kan weliswaar op haar lichaamsreserves interen, maar om nog enigszins aan haar energiebehoefte te voldoen, moet ze fourageren tijdens korte perioden dat ze van het nest afgaat. In **Box C** onderzoeken we bij een Nederlandse broedkolonie de lengte en frequentie van perioden dat het vrouwtje niet broedt ('incubatie reces'). We laten zien dat de Nederlandse vrouwtjes, ondanks een milder klimaat, minder tijd van het nest afgaan dan vrouwtjes van de Barentszzee. In **hoofdstuk 7** kijken we hoe voedselbronnen worden gebruikt tijdens het broedseizoen. Brandganzen van gematigde gebieden blijken een hoger lichaamsgewicht bij het begin van de incubatieperiode en een hoger gewichtsverlies tijdens het broeden te hebben dan de Arctische soortgenoten. Daarnaast laten we zien dat een groter gewichtsverlies bij ganzen van gematigde gebieden bepaald wordt doordat de eiwitvoorraden in het lichaam sneller opraken, terwijl het vetverbruik gelijk is aan dat van de brandganzen die in de Arctis broeden. Ook laten we zien dat de legselgrootte toeneemt van noord naar zuid terwijl de grootte van het ei afneemt. Waarschijnlijk profiteren de ganzen in het zuiden van lagere transportkosten (Arctische broedvogels moeten lichaamsreserves 'meezeulen' naar de broedgebieden) en een groter voedselaanbod in het begin van het broedseizoen dat hen in staat stelt meer eieren te leggen.

Men veronderstelt dat voedselplanten van cultuurgraslanden, ondanks het feit dat ganzen deze gebieden zeer aantrekkelijkheid blijken te vinden, een minder gunstige samenstelling van nutriënten hebben dan voedselplanten van de kwelder (hun natuurlijke voedselhabitat). Dit ongunstige dieet voor ganzen zou vervolgens nega-

tieve gevolgen voor de opbouw en de samenstelling van hun lichaamsreserves en uiteindelijk ook voor hun broedsucces hebben. **Box D** laat echter zien dat de samenstelling van lichaamsreserves in het voorjaar hetzelfde is voor dieren die 'opvetten' in cultuurgrasland als voor dieren die gebruik maken van de kwelder. De opbouw van eiwitten (spierweefsel) bleek een belangrijk deel uit te maken van het toegenomen lichaamsgewicht (24-33% op basis van versgewicht).

In **hoofdstuk 8** breng ik de resultaten van voorgaande hoofdstukken samen en geef aanvullende informatie. Het 'opvetten' van ganzen, d.w.z. het verkrijgen van lichaamsreserves, verdient extra aandacht. Een vergelijking van historische en recente gegevens over het lichaamsgewicht van brandganzen versterkt het vermoeden dat mogelijkheden om in het Waddenzeegebied in het voorjaar op te 'vetten' aanzienlijk zijn verbeterd gedurende de afgelopen decennia. Het is nog onduidelijk hoe het verschil in stikstofretentie bij brandganzen is te verklaren als ze foerageren in cultuurgrasland in vergelijking met kweldergebieden. Om stikstofbalansen correct naar eiwitbalansen te kunnen vertalen is meer inzicht nodig over de herkomst van de in het voedsel gemeten stikstof. Hoe dan ook, het idee van een verschil in de samenstelling aan aminozuren van de voedselplanten blijkt niet van toepassing te zijn.

Brandganzen, met hun recente kolonisatie van broedgebieden langs een grote ecologische gradiënt, lijken een zeer geschikt model systeem om mechanismen te onderzoeken wanneer organismen zich moeten aanpassen aan nieuwe leefgebieden. Meer inzicht hierin is hard nodig om te kunnen inschatten hoe dieren al dan niet met de uitdagingen kunnen omgaan die de huidige 'global change' met zich meebrengt.

Zusammenfassung

Zeit- und Energiemanagement
Alles Leben auf der Erde benötigt Energie und Nährstoffe (im Folgenden auch einfach „Ressourcen“ genannt). Die Effizienz mit der Organismen in der Lage sind diese grundlegenden Ressourcen auszubeuten und zu verwenden, hat direkte Auswirkungen auf ihre individuelle Fitness, also ihr Überleben und ihren Fortpflanzungserfolg. Ressourceansprüche variieren während des jährlichen Zyklus, wobei die Fortpflanzungsperiode eine zentrale Stellung einnimmt, da die Produktion von Nachkömmlingen zusätzliche, und teilweise womöglich sehr spezifische, Ressourcen erfordert. Des Weiteren zeigen die meisten Lebensräume auf unserem Planeten deutliche jahreszeitliche Schwankungen in der Verfügbarkeit von Ressourcen. Als Folge davon unterliegen Organismen einem starken Selektionsdruck, ihre jeweiligen Nahrungsansprüche mit der zeitlich variierenden Verfügbarkeit optimal abzustimmen. Kurzum, um Fitness zu maximieren, ist ein optimales Zeit- und Energiemanagement nötig.

Vor- und Nachteile wandernder Vögel
Die Flugfähigkeiten von Vögeln ermöglichen ihnen Ressourcen über große geographische Entfernungen hinweg zu integrieren. Die Phänologie von Nahrungsressourcen verläuft entlang klimatischer Gradienten und weist damit ein starkes räumlich-zeitliches Muster auf. Zugvögel können davon profitieren. Der sogenannten „green wave“ Hypothese zufolge stimmen arktische Gänse ihren Frühjahrszug in die Brutgebiete ab mit den lokalen Höhepunkten der Nahrungsqualität in aufeinanderfolgenden Rastplätzen entlang des Zugweges. So profitieren sie von stets günstigen Bedingungen (den ersten frischen gut verdaulichen Trieben), um sich reichliche Körpervorräte (besonders Fett und Protein) anzulegen. Diese Körperreserven erlauben es ihnen gegen Ende des Zuges der „Grünen Welle“ vorauszueilen, um in den großenteils noch schneebedeckten Brutgebieten mit der Brut so früh zu beginnen, dass der lokale Nahrungshöhepunkt mit dem Schlupf der Jungen zusammenfällt.

Allerdings bringen diese Vorteile des Wanderlebens auch Kosten mit sich. Das Einfügen von Zugperioden in den jährlichen Zyklus kostet extra Zeit und Energie, und erfordert damit wichtige Anpassungen in deren Management. Die Wanderung selbst birgt zusätzliche Gefahren (Erschöpfung, Räuberdruck, Wetter), und schließlich sind die meisten Zugvögel auf ganz spezifische Rastplätze angewiesen. Diese Abhängigkeit macht sie anfällig für Störungen in diesen, oft kleinräumigen, Rastgebieten.

Flexibilität und Grenzen in der Zug- und Brutbiologie der Nonnengans

Diese Dissertation beschäftigt sich mit dem Erwerb und der Nutzung von Nahrungs- und Energieressourcen, sowie der Zeitplanung bei Nonnengänsen *Branta leucopsis* während des Frühjahrzuges und in der Brutzeit. Nonnengänse der hier untersuchten Population überwintern entlang der Wattenmeerküste und ziehen traditionell im Frühjahr zu Rastplätzen an der Ostsee (Gotland, Öland, Estland) und dem Weißen Meer, um schließlich zu ihren russisch-arktischen Brutgebieten an der Barents See im äußersten Nordosten Europas (Nowaja Semlja, Waigatsch, Petschora-Delta) zu gelangen. Diese Population zeigte in den vergangenen Jahrzehnten einige bemerkenswerte Entwicklungen.

1) Seit den 1950er Jahren, als die Winterpopulation nur noch etwa 20000 Individuen zählte, zeigte sie anhaltendes exponentielles Wachstum und zählt derzeit mehr als eine halbe Million Vögel. 2) Seit den frühen 1990er Jahren registrieren wir zunehmend spätere mittlere Abzugszeiten (von bis zu 4 Wochen) aus dem Winterquartier am Wattenmeer für einen zunehmenden Anteil der Vögel. 3) Lange als typischer Brutvogel der hohen Arktis betrachtet, hat sich diese Spezies innerhalb der vergangenen drei Jahrzehnten eine Vielfalt von Bruthabitaten in den gemäßigten Breiten erschlossen und dadurch Entfernungen zwischen Brut- und Wintergebieten von vormals ca. 3500 km beachtlich verkürzt. Seit etwa 20 Jahren hat sich sogar eine im Wintergebiet sesshafte, und schnell wachsende, Brutpopulation etablieren können. Überdies scheint diese südwärts gerichtete Ausdehnung im Widerspruch zu einer vom Treibhauseffekt zu erwartenden Verschiebung nach Norden zu stehen. Diese bemerkenswerten Änderungen werfen Fragen auf über die Flexibilität in der Zeitplanung von Zug- und Brutgeschehen. Sind mit den verschiedenen Zugstrategien unterschiedliche Kosten und Nutzen verbunden? Inwieweit sind die Tiere imstande sich an neue (Brut-) Umgebungen anzupassen?

Obwohl die Bedeutung von Zug und Fortpflanzung als eng ineinander greifende Prozesse mittlerweile viel Beachtung findet, ist es bisher nur selten gelungen, die Zugmuster individueller Tiere auf ihren langen Wanderungen zu registrieren und in direktem Zusammenhang mit Geschehen im Brutgebiet zu setzen. Mit den Studien an Nonnengänsen aus den Brutgebieten in der russischen Arktis versucht die vorliegende Dissertation diese Wissenslücke wohl nicht völlig zu schließen, jedoch ein stückweit aufzufüllen. Ein anderes zentrales Thema dieser Dissertation befasst sich mit dem intraspezifischen Vergleich bedeutender „life history" Kennwerte (z.B. Gelegegröße und Überlebensrate) von Vögeln aus der russisch-arktischen Brutpopulation (Barentssee) und aus zwei Populationen in den gemäßigten Breiten

(Ostsee und Nordsee). Aufgrund der unterschiedlichen ökologischen Standortbedingungen in diesen Gebieten erwarten wir unterschiedliche Selektionsdrücke.

In den meisten unserer Studien liegt der Fokus auf dem erwachsenen, fortpflanzungsreifen Weibchen der Nonnengans. Im Zusammenhang mit Zeit- und Ressourcemanagement (vor allem von Körpervorräten) bei der Fortpflanzung kommt dem Gänseweibchen die größte Rolle zu. Außerdem entscheidet bei Gänsen vor allem das Weibchen über die Wahl des Brutplatzes.

Nach einem einleitenden Kapitel (Kap. 1) ist die Dissertation in drei Teile gegliedert und endet mit einer Synthese der Gesamtergebnisse einschließlich einiger Forschungsperspektiven (Kap. 8).

Teil I: Werkzeuge und Techniken

Dieser Teil beschreibt die wichtigsten Techniken, die uns erlaubten individuelle Vögel durch Raum und Zeit zu folgen und ihren Auf- und Abbau von Körpervorräten zu studieren. **Box A** informiert über die zwei Meßsysteme mit denen wir die Zugabläufe individueller Nonnengänse registrierten: Satellitentelemetrie mit implantierten Sendern und „Global Location Sensing" (GLS) mithilfe von an Beinringen befestigten Datenloggern (die Positionsbestimmung beruht auf der Messung von zeitgenauen Lichtwerten). Im Verlauf der Untersuchungsperiode von 2-3 Jahren ab Zeitpunkt des Anbringens der Geräte fanden wir keinen Unterschied in der Überlebensrate der Träger dieser Apparate im Vergleich zu Vögeln die lediglich mit farbmarkierten Fußringen ausgestattet waren. Weiterhin waren die zeitlichen Abläufe von Zug- und Brutgeschehen bei Vögeln mit und ohne diesen Geräten sehr vergleichbar (Kap. 3 und 4). Wir erachten daher die erhaltenen Messergebnisse als repräsentativ für die untersuchte Population. Diese automatischen Überwachungstechniken wurden von einem umfangreichen Beringungsprogramm ergänzt, das alle drei Studiengebiete (Barents-, Ost-, und Nordsee) einbezog. Somit waren direkte Beobachtungen an individuell markierten Vögeln in den Brut- und Überwinterungsgebieten möglich, die uns wichtige Informationen, wie z.B. zu Überlebensraten, lieferten (Kap. 6).

In **Kapitel 2** kalibrieren und evaluieren wir eine Isotopen-Verdünnungs-Methode (gegenüber der direkten Analyse am Kadaver). Eine mit Deuterium Isotopen markierte wässrige Lösung wird dem Tier gespritzt, und nach vollzogener Mischung mit den Wassermolekülen im Körper kann über den Verdünnungsgrad der markierten Moleküle in einer Blutprobe auf die Gesamtmenge an Körperwasser geschlossen werden. Die Menge Körperwasser kann wiederum benutzt werden, um Fett und fettfreie Masse abzuschätzen. Diese Technik erlaubt eine nicht-destruktive Analyse der Körperzusammenstellung und wurde benutzt, um die Ergebnisse in Kapitel 7 und Box D zu versammeln. **Box B** behandelt einige zusätzliche Ergebnisse der direkt am Kadaver gemessenen Zusammenstellung auf Organniveau. Der so ermittelte Wassergehalt im fettfreien Muskelgewebe wurde später für Umrechnungen zwischen Frisch- und Trockengewichten und bei der Schätzung von Protein- und Stickstoffbalancen verwendet (Kap. 7, Box D).

Teil II: Wandern um zu brüten

In 2004 registrierten wir mithilfe der GLS Logger erstmals Zugabläufe von Nonnengänsen auf ihrem Weg ins arktisch-russische Brutgebiet und beschreiben diese in **Kapitel 3**. Die meisten unserer „Loggervögel" verzogen erstaunlich spät aus ihrem Überwinterungsgebiet, bis zu vier Wochen später im Vergleich zum beobachteten mittleren Abzugsdatum 10 Jahre zuvor. Die Gänse reduzierten ihre Aufenthaltsdauer in den baltischen Rastgebieten gemäß ihrem (verspäteten) Abzug vom Wattenmeer, so dass die am spätesten ziehenden Vögel die traditionellen Rastplätze in der Ostsee gleichsam überflogen, welche in früheren Jahren von der gesamten Population genutzt wurden. Der Abzug aus der Ostsee war jedoch vergleichbar mit früheren Abzugszeiten. Ungeachtet inwieweit individuelle Vögel Gebrauch machten von baltischen Rastgebieten (traditionelle Strategie) oder nicht (neue Strategie), verbrachten sie alle eine bemerkenswert konstante Periode von ca. drei Wochen in arktischen Rastgebieten (vor allem am Dvina Fluss und auf der Halbinsel Kanin) bevor sie schließlich zur Brut schritten.

In **Kapitel 4** erforschen wir die Änderung in der Zugstrategie genauer, unter Benutzung von langjährigen Zähldaten zum Frühjahrszug und zu Populationsstärken, und im Verband mit Temperaturdaten. Die mit Hilfe von Loggern und Satellitensendern versammelten Zugdaten aus zwei Jahren (2004-05) geben uns Einsicht in die intraindividuelle Variabilität von Zugabläufen zwischen den Jahren, und ob die alternativen Zugstrategien Auswirkungen auf den Brutbeginn haben. Unsere Studien lassen eine bemerkenswerte Flexibilität im Zugablauf der Nonnengans sehen. Obwohl alle Vögel die gleiche Brutkolonie aufsuchten, waren ihre Abzugszeiten aus dem Wintergebiet über eine Periode von acht Wochen verteilt. Ein Individuum wechselte sogar von der traditionellen zur neuen Strategie (Reduktion oder Verzicht der Rast in der Ostsee zugunsten eines längeren Verbleibs im Wattenmeer), wobei es im zweiten Jahr die Wattenmeerküste 45 Tage später verließ als im Jahr zuvor. Wir vermuten, dass die Gänse mit der neuen Zugstrategie auf verschlechterte Bedingungen durch erhöhte Nahrungskonkurrenz in den baltischen Rastplätzen reagieren. Einem analytischen Rechenmodell aus der Flugmechanik zufolge sollten die Gänse die neue Strategie bevorzugen sobald die „fuel deposition rates" (Zunahmeraten von Körpervorräten) in der Ostsee im Vergleich zum Wattenmeer unter 88% fallen. Bisher können wir keine negativen Auswirkungen auf die Fortpflanzungschancen der Gänse die der neuen Strategie folgten entdecken. So war der Beginn der Eiablage (ein wichtiger Einflussfaktor des Bruterfolges) unabhängig vom Abzugsdatum aus dem Wintergebiet. Außerdem wuchs der Anteil der Vögel mit der neuen Strategie stetig in den letzten 15 Jahren, während die gesamte („flyway") Population ein ungebrochenes exponentielles Wachstum zeigte. Offenbar haben es die Gänse durch Änderungen in Platz- und (Nahrungs-) Habitatwahl geschafft, sich optimal über die im gesamten Nord-Ostsee-Raum verfügbaren Ressourcen zu verteilen, um somit dem Sättigungsproblem der baltischen Rastplätze auszuweichen.

Kapitel 5 bespricht die Bedeutung der auf Frühlingsrastplätzen angelegten Nahrungs- und Energiereserven für die Fortpflanzung bei arktischen Gänsen. Wir

betonen die Notwendigkeit ausreichender Körpervorräte für die Bebrütungsperiode, welche die (zusätzlichen) Ressourcen für die Produktion des Geleges bei Weitem übersteigen. Diese totalen Brutkosten können über die Nahrungsaufnahme in den Brutgebieten allein nicht gedeckt werden, sondern müssen zu einem erheblichen Teil von Körpervorräten geliefert werden, die zuvor auf Frühlingsrastplätzen angelegt wurden.

Teil III: Warum wandern um zu brüten: ein Nord-Süd-Vergleich
Schwerpunkt in **Kapitel 6** bilden das Timing der Fortpflanzungsperiode und der Fortpflanzungserfolg. Die Nonnengänse im Nord- und Ostseeraum brüten 6 bis 7 Wochen früher als ihre Artgenossen in der Arktis. Wir zeigen, dass für die meisten der arktischen Vögel die Brutzeit zusammenfällt mit der Periode in der die meisten Jungen produziert werden, wohingegen die meisten der Brutvögel im Nord- und Ostseeraum noch stets zu spät brüten, um maximalen Fortpflanzungserfolg zu erzielen. Letztere scheinen an die neuartige (südliche) Brutumgebung noch nicht völlig angepasst zu sein, beziehungsweise stoßen an Grenzen, die ihnen ein optimales Anpassen erschweren oder gar unmöglich machen. Auf der anderen Seite ist die Überlebensrate von Jungtieren bis zur Ankunft im Überwinterungsgebiet viel geringer bei den arktischen Vögeln, was das Risiko der Wanderung verdeutlicht.

Während der Bebrütungsphase ist die Nahrungsaufnahme beim Weibchen stark eingeschränkt. Dann zehrt es zu einem großen Teil von Körpervorräten, muss aber regelmäßige Bebrütungspausen einlegen, um für zusätzliche Nahrungszufuhr zu sorgen. In **Box C** untersuchen wir Häufigkeit und Dauer dieser Bebrütungspausen für Weibchen der niederländischen Brutkolonie. Außerdem zeigen wir, dass die niederländischen Gänse, trotz des wärmeren Klimas, insgesamt weniger Zeit mit Bebrütungspausen zur Nahrungsaufnahme zubringen als ihre Artgenossen von der Barentssee. **Kapitel 7** beschäftigt sich mit der Ressourcennutzung während der Fortpflanzung. Die Nonnengänse aus den südlichen Brutkolonien haben eine größere Körpermasse zu Beginn der Bebrütungsphase, verbrauchen aber bis zum Schlupf der Jungen auch mehr von ihren Körpervorräten als Brutvögel aus der Arktis. Der höhere Verlust an Körpermasse bei den Vögeln im Süden ist dem Abbau von Proteinen zuzuschreiben, wohingegen die verbrauchte Menge Körperfett ähnlich groß war wie bei den arktischen Brutvögeln. Ein Vergleich von Ei- und Gelegegröße zwischen drei Brutpopulationen weist auf einen geographisch gegenläufigen Trend hin: während die Größe der Eier von Norden nach Süden abnimmt, nimmt die Gelegegröße zu. Wahrscheinlich profitieren die südlichen Brutvögel von geringeren Transportkosten (arktische Vögel müssen Körpervorräte aus dem Süden mit sich nehmen) und einer größeren Nahrungsverfügbarkeit zu Begin der Brutzeit, wodurch sie in der Lage sind mehr Eier zu legen.

Früheren Untersuchungen zufolge wird angenommen, dass Gräser der landwirtschaftlichen Grünlandflächen, die von Gänsen zunehmend genutzt werden, den Vögeln eine schlechtere Nährstoffzusammensetzung bieten als Futterpflanzen in ihrem natürlichen Habitat (den Salzgraswiesen) , mit negativen Folgen für den

Aufbau von Körpervorräten und schließlich den Bruterfolg. In **Box D** wird der Aufbau von Körperreserven während der Frühlingsrast untersucht für Nonnengänse, die intensiv bewirtschaftetes Grünland oder natürliche Salzgraswiesen als vornehmliches Nahrungshabitat nutzen. Die Gänse aus diesen zwei Habitaten unterschieden sich nicht in ihrer Körperzusammenstellung. Ein beachtlicher Teil der zugelegten Körpermasse bestand aus Protein (24-33% der Körperfrischmasse).

In **Kapitel 8** integriere ich, gestützt von zusätzlichen Informationen, Ergebnisse und Schlussfolgerungen der vorangehenden Kapitel. Dem Erwerb von Körpervorräten wird dabei besondere Aufmerksamkeit geschenkt. Vieles weist daraufhin, dass Nonnengänse während der Frühlingsrast im Wattenmeergebiet (einschließlich der küstennahen Binnenlandrastgebiete) die Rate des Aufbaus von Körpervorräten in den letzten Jahrzehnten deutlich erhöhen konnten. In der Diskussion rund um die Futterqualität von landwirtschaftlichen Grünlandflächen gegenüber natürlichen Salzgraswiesen stellt die unterschiedliche Stickstoffrückhaltung bei Gänsen in diesen Nahrungshabitaten ein noch weitgehend ungelöstes Problem dar. Die Idee einer unterschiedlichen Zusammensetzung an Aminosäuren in den jeweiligen Futterpflanzen erweist sich allerdings als unwahrscheinliche Erklärung für die beobachteten Unterschiede.

Die Nonnengans, mit ihren rezent über große Breiten hinweg etablierten Brutpopulationen, könnte ein vielversprechendes Modelsystem für mehr Forschung zu den Mechanismen der Anpassung an neue Lebensräume bieten. Ein tieferes Verständnis davon ist dringend nötig, um einschätzen zu können inwieweit Organismen in der Lage sind mit den Herausforderungen des globalen Wandels zurechtzukommen.

Резюме

Распределение времени и энергии

Все живые организмы нуждаются в энергии, которую они получают за счет расщепления питательных веществ, поступающих из окружающей среды. Их жизнеспособность и репродуктивные качества напрямую связаны с эффективностью использования энергетических ресурсов. Потребность в энергетических ресурсах варьирует на протяжении годового цикла и резко возрастает в период размножения, когда энергия необходима не только для взрослых особей, но и для растущего потомства. Более того, доступность ресурсов в большинстве биотопов сильно варьирует в зависимости от сезона. Таким образом, синхронизация потребности в энергетических ресурсах и их доступности в существенной мере подвержена влиянию отбора. Иными словами, приспособленность в значительной степени означает оптимизацию распределения времени и энергии.

Затраты и выгоды миграции птиц

Способность птиц к полету дает им возможность занимать обширные ареалы. Перелетные птицы могут следовать за пиком доступности ресурсов, смещающимся вдоль климатического градиента. Так, предполагается, что гнездящиеся в Арктике гуси приурочивают свою весеннюю миграцию к «зеленой волне» ранневесеннего (наиболее питательного) прироста травы вдоль пути миграции. На местах остановок на пути миграции они, за счет интенсивной кормежки, пополняют энергетические затраты на перелет и запасают вещества (в основном жир и протеин), которые впоследствии понадобятся для формирования яиц. Накопление энергетических ресурсов на местах остановок позволяет мигрантам опережать в конце пути волну сезонного обилия пищи и, таким образом, синхронизировать период выкармливания выводков с местным пиком обилия ресурсов.

Однако эти выгоды имеют свою цену. Добавление миграционных эпизодов к годовому циклу происходит за счет увеличения расходов и времени, и энергии. Более того, из-за хищничества и других опасностей, которые подстерегают птиц, миграция может сопровождаться высокой смертностью по сравнению с другими фазами годового цикла. Наконец, многие мигранты рассчитывают на многочисленные, зачастую, весьма специфичные, места остановок для жиронакопления. Эта зависимость делает их уязвимыми к деградации таких критических точек или к беспокойству на них.

Гибкость и ограничения в миграции и размножении белощёкой казарки

Целью диссертации является изучение рационализации использования времени и аспектов приобретения и потребления ресурсов белощёкими казарками *Branta leucopsis* во время весенней миграции и периода размножения. Популяции белощёкой казарки, которые зимуют вдоль побережья Ваттового моря и традиционно мигрируют через места остановок на Балтике к местам размножения на Русском Севере, замечательны по крайне мере в трех отношениях.

Во-первых, после спада численности в 1950-х гг., когда популяция составляла всего около 20,000 особей, вся популяция, использующая данный пролетный путь, к настоящему времени экспоненциально возросла до полумиллиона особей. Во-вторых, с начала 1990-х гг. возрастающая часть популяции откладывает отлет из районов зимовки в Ваттовом море (в данный момент примерно на четыре недели). В-третьих, этот вид, который долгое время считался облигатно арктической гнездящейся птицей, за последние три десятилетия

колонизировал различные биотопы в умеренных широтах, таким образом существенно сократив дальность миграции или даже вовсе прекратив мигрировать. Более того, эта экспансия кажется противоречащей ожидаемому распространению в более северные районы из-за глобального потепления. Эти примечательные изменения поднимают вопросы относительно гибкости сроков миграции и размножения. Каковы плюсы и минусы разных стратегий миграции? И, в контексте глобальных изменений, до какой степени животные способны адаптироваться к быстро изменяющейся окружающей среде?

Хотя сейчас широко признано, что миграция и размножение тесно связаны, наблюдение за процессами дальней миграции у птиц на индивидуальном уровне и их связью с процессами в период размножения редко удавалось провести. В данной диссертации сделана попытка закрыть эту информационную брешь для мигрирующей популяции белощёкой казарки, гнездящейся в российской Арктике. Другой центральной темой диссертации является внутривидовое сравнение основных показателей у популяций гнездящихся вдоль большого экологического градиента от арктических до умеренных условий и испытывающих разное давление отбора.

Основной упор сделан на взрослых половозрелых самок белощёкой казарки. Причиной этого является прежде всего центральная роль гусынь в управлении временем и ресурсами для размножения. Кроме того, у гусей самка выбирает место размножения.

После вводной главы, диссертация разделена на три основные части, и заканчивается общим обсуждением результатов и перспектив дальнейших исследований.

Часть I. Материалы и методы

В этой части описаны методы, которые мы использовали для прослеживания отдельных птиц в пространстве и времени, и для изучения накопления и расходования ими резервов энергии. **Врезка A** описывает две системы прослеживания, которые мы использовали для мониторинга дальних миграционных перемещений особей, гнездящихся в российской Арктике: спутниковая телеметрия с использованием имплантированных передатчиков и глобальная запись локаций (GLS) с использованием чипов, прикрепленных к кольцу. За время исследований (2-3 года с момента прикрепления устройств) мы не обнаружили воздействия на выживаемость казарок, которое могло бы быть вызвано использованием прослеживающих устройств. Более того, из-за ярко выраженной синхронности времени миграции и размножения птиц с устройствами и без устройств (гл. 3 и 4) мы уверены, что собранные нами данные репрезентативны для птиц в изучаемой популяции. Эти программы индивидуального прослеживания дополнялись обширной программой кольцевания, включавшей все три изучаемые популяции. Прямые наблюдения маркированных птиц поставляли информацию относительно выживаемости и индивидуального успеха размножения.

В **главе 2** мы описываем калибровку и оцениваем метод разведения изотопа дейтерия как прижизненный метод оценки содержания воды, жира и сухого нежирового компонента в теле белощёких казарок. Этот метод был важным инструментом исследования, результаты которого представлены в гл. 7 и врезке D. Во **врезке B** представлены детали каркасного анализа отдельных органов. Содержание воды в нежировой мышечной ткани использовалось для оценки баланса белка и азота (гл. 7, врезка D).

Часть II. Путешествие для размножения

Первые данные о графике весенней миграции для самок из гнездовой колонии в России, снабженных чипами GLS, были получены в 2004 г. и представлены в **главе 3**. Большинство прослеженных нами птиц были пионерами новой стратегии и значительно отложили отлет из районов зимовки в Ваттовом море (до четырех недель) по сравнению со временем массового отлета в прежние годы. Продолжительность остановок в Прибалтике была сокращена в соответствии с поздним отлетом с Ваттового моря, так что поздно начавшие миграцию птицы практически проскочили балтийские места остановок, которые традиционно использовались все популяцией. Однако все птицы провели одинаковое количество времени (ок. трех недель) в арктических местах остановок до начала гнездования.

В **главе 4** мы более подробно рассматриваем изменения в расписании весенней миграции, используя многолетние данные весенних учетов, учетов численности популяции и температурные данные. Мы также применили аналитическую модель, основанную на теории оптимальной миграции, чтобы оценить условия скорости накопления жира, при которых отказ от остановки на Балтике может быть выгодным. Данные, собранные с помощью GLS и спутникового прослеживания за две сезона (2004 и 2005), позволяют также рассмотреть межгодовую вариацию сроков весенней миграции у отдельных особей, и выяснить, приведет ли использование альтернативной миграционной стратегии к изменению времени размножения. Наши данные указывают на ярко выраженную гибкость в сроках миграции. Различия в сроках покидания района зимовки особями, гнездящиеся в одной колонии в Арктике, могут достигать восьми недель, и даже одна особь может решить начать миграцию на 45 дней позже, чем в предыдущем году. Мы предполагаем, что новая стратегия миграции появилась в ответ на возросшую пищевую конкуренцию в местах остановки в Прибалтике. Нам пока не удалось обнаружить явных признаков буферного эффекта, связанного с насыщением прибалтийских районов, который бы негативно влиял на птиц, которые используют недавно возникшую альтернативную стратегию позднего отлета с Ваттового моря. Время откладки яиц (надежный предиктор будущего успеха размножения) было одинаковым у птиц, которые оставались в Ваттовом море и у тех, что останавливался на Балтике, и в то время как доля первых возрастала, размер всей популяции увеличивался в геометрической прогрессии. По-видимому, широкомасштабные изменения в использовании районов жиронакопления и биотопов позволило казаркам оптимально использовать ресурсы, доступные им весной в североморско-балтийском регионе и таким образом избежать негативных последствий зависимости от плотности.

В **главе 5** рассматривается важности весенних остановок для репродуктивных перспектив гнездящихся в Арктике гусей. Мы подчеркиваем потребность в ресурсах, необходимых для успешного завершения насиживания, которая намного превышает (дополнительные) потребности для формирования яиц. Эти потребности не могут быть обеспечены только за счет питания в местах размножения, а должны в значительной степени обеспечиваться запасами, накопленными в местах остановок до достижения районов размножения.

Часть III. Зачем путешествовать для размножения: сравнение размножения в Арктике и в умеренных широтах

В этом разделе мы сравниваем три популяции белощёкой казарки: одну арктическую (Баренцево море) и две гнездящиеся в умеренных широтах (на Балтийском и Северном морях). В **главе 6** основное внимание уделено срокам

размножения в арктической популяции совпадает с периодом максимальной продукции молодняка, в то время как популяции умеренных широт в данный момент, как кажется, не полностью адаптированы к новой окружающей среде. Мы предполагаем, что, по-видимому, существуют ограничения, не позволяющие птицам в умеренных широтах гнездиться и линять раньше. Несмотря на это, выживаемость молодых птиц до прибытия в район зимовки (оцененная методом мечения – повторного отлова) в арктической популяции намного ниже, что указывает на опасности миграции.

Насиживание – это период сильнейшего энергетического стресса для самки, когда из-за необходимости насиживать она должна в большой степени полагаться на накопленные запасы энергии. Самка дополнительно удовлетворяет свою потребность в ресурсах за счет кормежки во время перерывов в насиживании. Во **врезке C** мы рассматриваем частоту и продолжительность эпизодов кормежки в зависимости от дня насиживания для самок из гнездовой колонии в Нидерландах. Мы также показываем, что, несмотря на более высокие температуры, голландские самки проводят меньше времени вне гнезда, чем самки из популяции Баренцева моря. В **главе 7** мы рассматриваем использование ресурсов во время размножения. Белощёкие казарки, гнездящиеся в умеренном климате, начинают насиживание, имея более высокую массу тела, и теряют больше веса во время насиживания, чем птицы, гнездящиеся в Арктике. Мы разделяем потери жира и белка с помощью изотопных измерений (метод, описанный в главе 2) и показываем, что скорость потери массы тела у казарок в умеренных широтах высока из-за расхода белка, в то время как расходование жира в двух популяциях находится на сходном уровне. Мы также показываем существование противонаправленных широтных градиентов в размере кладки и размерах яиц: размер кладки увеличивается по направлению с севера на юг. В умеренных широтах казарки могут в большей степени, чем в Арктике, полагаться на текущую кормежку при формировании яиц, тем самым экономя внутренние запасы. Вместе с меньшим размером запасов энергии у мигрирующих гусей в момент откладки яиц из-за расходов на перелет, это является возможным объяснением уменьшения размера кладки с широтой.

Высказывалось предположение, что несмотря на внешнюю привлекательность для гусей, кормежка на полях предоставляет им менее ценный набор питательных веществ, чем кормежка на соленых маршах, и тем самым влияет на состав запасов энергии, накапливаемых во время весенней кормежки, в конце концов негативно влияя на успех размножения. Во **врезке D** рассматривается накопление запасов энергии во время весенних остановок на сельскохозяйственных полях по сравнению с соленым маршем на голландском острове Схермонникоог (Schiermonnikoog). Состав тела казарок, кормившихся в этих двух биотопах, был сходен. Масса сырого протеина составляла существенную долю (от четверти до трети) увеличения массы тела.

В заключительной **главе 8** я обобщаю результаты полученные в предыдущих главах и обсуждаю их в свете дополнительной информации. Особое внимание уделяется накоплению запасов энергии. Сравнение исторических и современных данных по динамике массы тела белощёких казарок поддерживает точку зрения, что возможности жиронакопления в Ваттовом море в последние десятилетия улучшились. В дискуссии о питании в сельскохозяйственных угодьях и в естественных биотопах нерешенной проблемой остается разная усвояемость азота, обнаруженная в этих биотопах. Однако ранее выдвигавшиеся в качестве причины различия в аминокислотном составе кормовых растений вряд ли могут объяснить наблюдаемые различия.

Я заканчиваю обзором перспектив изучения белощёких казарок, которые представляют удобную систему для более подробного изучения механизмов адаптации к образам жизни на разных широтах, тем самым углубляя наши представления о том, как организмы могут решать проблему приспособления к глобальным изменениям или отказываться от ее решения.

Rudi at work was photographed by E. Gurtovaya.

Acknowledgements

I believe that dissertation work is a challenge for every PhD student, and it ought to be. However, such work is seldom the result of efforts by a sole person. Here I want to thank a number of people who helped me to master this challenge, in particular those people I did not mention in the acknowledgements of the previous chapters.
Probably as many other students before me, I was captured by one of Rudi Drent's talks, on this occasion at a waterfowl conference in Moscow. Later, at the conference dinner, I saw Rudi standing up to call out loudly 'rabota! rabota! rabota!' (i.e., "work"), a phrase so familiar to one who grew up in Eastern Germany that my wish to work under his supervision was readily born and has been finally realised. Rudi gave me the freedom to find a research niche within the group and to develop and pursue my own interests. That my efforts took me somewhat longer than usually expected for a PhD period partly reflects a broad interest. Rudi always showed great faith in my ventures, and his steady optimism and enthusiasm have been a great motivation for me. I very much enjoyed the time we spent together on expeditions to Russia, including many lessons in diplomacy combined with great storytelling. Rudi, you have been a great "Doktorvater" to me. I also would like to thank Nel for the warm welcome I received during frequent visits at your home. Two other people crucial to get me 'into the boat' were Jan Bakker and Julia Stahl. Jan and Julia, I very much enjoyed the cheerful atmosphere you have created, and I sincerely thank you for all your help in front of or behind the scenes. Henk van der Jeugd has been a major and close collaborator in this thesis work. Among many other contributions he handled a huge ringing programme, which has been so vital for the barnacle goose work. Joost Tinbergen was always accessible when I encountered scientific problems, and I learned a lot from his scrutiny of my statistics. Jouke Prop introduced me to the realm of goose feeding ecology. His meticulous working style and unrivalled endurance in observing geese at freezing temperatures from a one cubic meter blind has become the archetype of fieldwork for me since our first common expedition to Kanin in 2002.

This dissertation work has involved a lot of data collection, which would not have been possible without many helping hands. I want to acknowledge the help I received from students from the Van Hall Institute and the RuG: Astrid Tijdens,

René Adelerhof, Michiel Schouten, Annelies Pouw, Jacintha van Dijk, and our Russian colleagues: Konstantin Litvin, Elena Gurtovaya, Julia Karagicheva, Yuri Anisimov and Dimitri Ochinashko (I will miss our nail throwing competitions), Olga Pokrovskaya and Olga Lavrinenko. I further relied upon the valuable skills of 'canon-Kees' Oosterbeek for the trapping of spring-staging geese on Schiermonnikoog. As most of the data collection took place in remote Arctic places located within the Russian border zone, our success crucially depended on special logistics and a great deal of other organizational work. Konstantin Litvin (Bird Ringing Centre Moscow) played always a major role in the preparations for our international field expeditions. I am also grateful to Mennobart van Eerden (RIZA) who introduced me to the Tobseda study site and greatly facilitated the work there through his established network of reliable local supporters. The following people and institutions from Naryan Mar, Nenets Autonomous Region, provided logistical support or helped with visa, permissions and registration formalities: Andrey Glotov (State Nature Reserve 'Nenetskii'), Alexander Kusnyetsov (State Hunting Inspection), Yana Kislyakova and Natalya Nerobova (State Committee for Environmental Protection). Further help came from Harald Leummens ('Partners for Water' program of the Dutch government) and Valery Andreyev (Nature Museum Arkhangelsk). In the Netherlands, Vereneging Naturmonumenten and Staatsbosbeheer provided permissions for work on Schiermonnikoog and at Hellegatsplaten, respectively. For additional logistical support I would like to thank Otto Overdijk, René van Loo and Ronald in 't Veld. In Haren Roelie and Sjoerd Veenstra took care of our goose stock at home.

Back from the field most of the data had yet to be retrieved from samples of various kinds. Most of the plant and goose dropping samples were analysed by Nelly Eck and Bert Venema from the COCON lab, Groningen and by the Chemical and Endocrinology lab led by Léon de Jonge from the Animal Science Group of the University of Wageningen. Marcel Klaassen (NIOO) welcomed me heartily to use the NIRS machine in his lab and, supported by Harry Korthals and Steffen Hahn, provided furthermore the analysis of stable isotopes. I am grateful to Harro Meijer and Berthe Verstappen-Dumoulin (CIO Groningen) who provided the analysis of deuterium enrichments, thereby continuing the collaborative work initiated by the late Henk Visser. Data collection for this thesis would have been unimaginable without the right material and special adjustments of instruments. For this I could happily rely on the "gouden handen" of Ger Veltman from the "Instrumentenmakerij". Jacob Hogendorf at COCON helped out with material and tools when urgently needed. At the British Antarctic Survey Vsevolod Afanasyev and James Fox were excellent partners in the venture of tracking birds by geolocation.

I would like to thank Franz Bairlein, Ron Ydenberg and Gilles Gauthier for their interest, time and comments on my thesis manuscript. Jeroen Creuwels, Nikita Chernetsov and Julia Karagicheva helped me with the Dutch and Russian summaries. Any congratulations on the visual attractiveness of the thesis I would like to forward to Dick Visser, who took care of layout and figures, and Jens Gregersen, for kindly allowing me to use one of his drawings on the cover.

I am grateful to all members of the Animal Ecology Group and a number of people from other departments for the inspiring and social atmosphere they created during my stay at the Biological Centre. Suus Bakker has been of invaluable help in meeting all the administrative demands. I want to thank Janske and Marion (my 'paranimfs'), Richard, Eelke, Cas & Karen, Martijn & Lyanne, Martijn & Martine, Martin & Steffi, Popko, Leo & Corine, Dries, Yvonne, Arne, Chris, Nick, Kevin, Debbie, Liz & Thor, Maaike, Julia & Martin, Luc, Elske, Deniz, Jeroen, Herfita, Ilja, Peter, Kristin, Vivian and Ralf for all the social events in or outside the BC. During times in the field it was 'erg gezellig' with Sandra, Reinout, Roos, Esther and Ciska. I had also a lot of fun together with the diving-fanatics from Calamari, either in the water or over some 'biertjes'. Finally I am thankful to 'Bureau Carex', and Lenze Hofstee and Linie Dijkstra in particular, for the provision of an affordable shelter over all those years. It has been a pleasure for me sharing the flat with Maarten Sonderen, and I want to thank him for the many inspiring discussions.

Last but not least, I want to thank my parents for raising me in one of Germany's best birding areas, and for their steady support and faith in all my endeavours.

Götz Eichhorn

Thanks to dog Ashley, who tried its best keeping our house (nearly) mouse-free.

List of publications

Papers in international refereed journals

Eichhorn G and Visser GH (2008) Evaluation of the deuterium dilution method to estimate body composition in the barnacle goose: accuracy and minimum equilibration time. Physiological and Biochemical Zoology (*in press*)

Schielzeth H, Eichhorn G, Heinicke T, Kamp J, Koshkin MA, Koshkin AV and Lachmann L (2008) Waterbird population estimates for a key staging site in Kazakhstan: a contribution to wetland conservation on the Central Asian flyway. Bird Conservation International 18: 71-86

Drent RH, Eichhorn G, Flagstad A, Van der Graaf AJ, Litvin KE and Stahl J (2007) Migratory connectivity in Arctic geese: spring stopovers are the weak links in meeting targets for breeding. Journal of Ornithology 148: S501-S514

Eichhorn G, Afanasyev V, Drent RH and Van der Jeugd HP (2006) Spring stopover routines in Russian barnacle geese *Branta leucopsis* tracked by resightings and geolocation. Ardea 94: 667-678

Goss-Custard JD, West AD, Yates MG, Caldow RWG, Stillman RAS, Castilla J, Castro M, Dierschke V, Le V dit Durell SEA, Eichhorn G, Ens BJ, Exo K-M, Fernando PUU, Ferns PN, Hockey PAR, Gill JA, Johnstone I, Kalejta-Summers B, Masero JA, Moreira F, Nagarajan R, Owens IPF, Pacheco C, Perez-Hurtado A, Rogers D, Scheiffarth G, Sitters H, Sutherland WJ, Triplet P, Worrall DH, Zharikov Y, Zwarts L and Pettifor RA (2006) Intake rates and the functional response in shorebirds (*Charadriiformes*) eating macroinvertebrates. Biological Reviews 81: 501-529

Van der Jeugd HP, Gurtovaya EN, Eichhorn G, Litvin KE, Mineev OYu and Van Eerden M (2003) Breeding barnacle geese in Kolokolkova Bay, Russia: number of breeding pairs, reproductive success, and morphology. Polar Biology 26: 700-706

Prinzinger R, Haubitz B, Eichhorn G and Nothwang U (2003) Comparative heart mass in Blue-naped Mousebirds (*Urocolius macrourus*) and Speckled Mouesebirds (*Colius striatus*). Ostrich 74: 139-140

Schielzeth H, Lachmann L, Eichhorn G and Heinicke T (2003) The white-headed duck *Oxyura leucocephala* in the Tengiz-Korgalzhyn Region, Central Kazakhstan. Wildfowl 54: 115-129

Gilg O, Sane R, Solovieva DV, Pozdnyakov VI, Sabard B, Tsanos D, Zoeckler Ch, Lappo EG, Syroechkovski Jr EE and Eichhorn G (2000) Birds and mammals of the Lena Delta Nature Reserve, Siberia. Arctic 53: 118-133

Eichhorn G and Heinicke T (2000) Notable observations of the sociable plover *Vanellus gregarius* from the Tengiz-Korgalzhyn area - central Kazakstan. Wader Study Group Bulletin 93: 73-76

Papers in non-refereed journals

Eichhorn G (2005) Breeding record of the red phalarope *Phalaropus fulicarius* in European Russia. Information materials of the working group on waders (Moscow) 18: 49-50

Eichhorn G and Khrokov VV (2002) Decline in breeding sociable plover *Chettusia gregaria* in the steppes of Naurzum and Korgalzhyn, Kazakhstan. Sandgrouse 24: 22-27.

Eichhorn G (2001) Semipalmated plover *Charadrius semipalmatus* - first confirmed record for the Asian Mainland. Information materials of the working group on waders (Moscow) 14: 31-33

Eichhorn G (2001) Observations of the semipalmated sandpiper *Calidris pusilla* at Mechigmenskaya Gulf, Chukotsky Peninsula. Information materials of the working group on waders (Moscow) 14: 33-34

Eichhorn G (2001) Observation of an abnormal coloured little grebe *Tachybaptes ruficollis* poggei (Reichenow, 1902) on Kunashir, Kuril Islands. Ornithologische Mitteilungen 53: 419-420

Tolvanen P, Eskelin T, Aarvak T, Eichhorn G, Oien IJ and Gurtovaya E (2000) Monitoring the autumn staging of lesser white-fronted geese in Kazakstan, October 1999. In: Tolvanen P, Oien IJ and Ruokolainen K (eds). Fennoscandian Lesser White-fronted Goose Conservation Project. Annual report 1999. WWF Finland Report 12 and NOF Rapportserie Report no. 1-2000

Volkov SV, Eichhorn G and Sofronov YuN (1998) Breeding of brent geese in the north of the Lena Delta in 1997. Casarca (Bulletin of the Goose and Swan Study Group of Eastern Europe and North Asia) 4: 120-128

Book chapters

Eichhorn G (2005) Northward bound: fat for flight: How barnacle geese budget their spring travels. In: Drent RH, Bakker JP, Piersma T and Tinbergen JM (eds). Seeking Nature's Limits: Ecologists in the Field. KNNV Publishing, Utrecht, pp 84-90

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