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Factors affecting the site of investment, and the reliance on savings for arctic breeders: the capital–income dichotomy revisited

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The extent to which migratory birds that breed in the Arctic and winter in southern biomes rely on residual body stores for reproduction is unresolved. The short arctic summer and the limited availability of food early in the season constrain the time available for successful reproduction. Birds that are able to bring sufficient endogenous reserves to the breeding ground to meet, at least partially, the demands of egg-laying can initiate clutch production soon after arrival, thereby shortening the length of the breeding season and improving the chances of reproductive success. The amount of reserves available will be influenced by body size, the increased energetic and predation costs associated with carrying large stores, distances between staging sites and the location of the breeding grounds within the Arctic. Birds need not fly directly to the breeding grounds from the established temperate staging sites. Extensive feeding by migrants may occur in the Arctic, even within a few kilometres of the breeding sites as the birds track the retreating snowline. Irrespective of their size, birds are thus able to store some resources necessary for egg laying at local or regional scales. It is thus important to make a distinction between local capital and distant capital breeding. The extent to which a bird is characterized as a distant capital, local capital, or an income breeder not only varies between species, but also between individuals and seasons.

Key words: capital and income breeders, body size, fat, protein, inter-annual and intra-specific variation in arrival and egg-laying dates

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INTRODUCTION

Migratory birds that nest early during the short arctic summer are often more successful than

those nesting later, resulting in a pattern of strong seasonal decline in reproductive success (Cooke *et al.* 1995, Lepage *et al.* 2000). However, birds arriving early in spring on the breeding grounds may



have restricted feeding opportunities, hence post-migratory body stores allow egg-laying to begin before local foods become available, thereby avoiding any delays in breeding and maximizing opportunities for reproductive success (e.g. Ryder 1970, Ankney & MacInnes 1978, Raveling 1979a,b, Ebbsing *et al.* 1982, Davidson & Evans 1988, Sandberg & Moore 1996). Drent & Daan (1980) introduced the terms 'capital' and 'income' breeding in bird populations to describe a dichotomy between birds relying on endogenous nutrients and those relying on exogenous nutrients. In the first case, females use body stores (capital) brought from the wintering grounds or migration areas to the breeding grounds to produce eggs. In income breeding, eggs are produced from nutrients obtained directly on the breeding grounds. Subsequently, many investigators have examined the extent of capital and income breeding (i.e. the degree of dependence on stored nutrient reserves for egg production) in migrant bird populations (details given below).

Trade-offs between capital breeding in arctic birds of different body size and opportunities for acquisition of nutrients and energy along the migration route, particularly at northern staging sites, have received comparatively little attention. Size-dependent predictions with respect to the occurrence of capital and income breeding in birds using allometric relationships for time, protein and energy demands during migration and breeding indicate capital breeding is likely to be prevalent only in large birds (Klaassen 2003). Most studies of capital and income breeders amongst long-distance migratory birds that breed in the Arctic have been based on geese (e.g. Ryder 1970, Ankney & MacInnes 1978, Ebbsing *et al.* 1982), but the possible occurrence of capital breeding in arctic-breeding waders (Davidson & Evans 1988) and passerines (Sandberg & Moore 1996) also has been investigated.

Originally, the distinction between capital and income breeding was based on the deposition of energy and protein in eggs (Drent & Daan 1980), but more recently all reproductive investment up to the time of hatch (i.e. self maintenance and

incubation) has been included in the assessment. In addition, the two types of breeding are now thought to represent extremes on a continuum of breeding strategies (Owen & Reinecke 1979, Bonnet *et al.* 1998, Meijer & Drent 1999). In this review, we first discuss the expected size dependency of capital breeding and its interaction with migratory strategies followed by a review of the available literature on a size range of species. Subsequently, we focus on geese and swans which, given their size, are the most likely candidates to adopt a capital breeding strategy *sensu* Drent & Daan (1980). Analysing the time lags between arrival and clutch-initiation dates on the breeding grounds, when nutrients for breeding can potentially be stored, in combination with evidence from stable-isotope studies, we examine whether their concept of capital and income breeding requires re-assessment. In particular, the origin of the 'capital', (i.e. at greater or shorter distances from the breeding grounds), is addressed.

Egg composition and body stores

Initially, we examine the costs of clutch production and the relationships between female body mass, egg size and clutch size. Female shorebirds (e.g. the Little Stint *Calidris minuta* with a body mass of c. 30 g and a 4-egg clutch size of 24 g; Cramp & Simmons 1983) are unable to produce a clutch from body stores alone. In contrast, large birds (e.g. a 9.1 kg Whooper Swan *Cygnus cygnus* which lays a 1.6 kg 5-egg clutch; Cramp & Simmons 1977) may be able to produce a clutch from body stores. The energy content of bird eggs (6.3–7.9 kJ g⁻¹; Sotherland & Rahn 1987) is only one-fifth to a quarter of the energy content of fuel stores needed for migration (Jenni & Jenni-Eiermann 1998), and migratory fuel stores do not have the same protein to fat ratio as eggs. On a dry weight basis, eggs contain approximately 60% protein (Sotherland & Rahn 1987), which is much higher than the 6–20% protein found in migratory fuel stores (Jenni & Jenni-Eiermann 1998, Klaassen *et al.* 2000). The latter are inadequate for egg synthesis, as they are deficient in protein. In addition, fat stores in adipose tissue used in migration contain

virtually no water, whereas protein is associated with as much as 77% water (Blaxter 1989). Because of this water content, large protein stores for egg synthesis would make body weight substantially heavier than the typical weight of birds at the start of migration. The stores (largely protein) needed to produce the 24-g clutch of the Little Stint amount to 17 g, whereas typical fuel stores (largely fat) for migration with the same energy density weigh only 6 g.

Thus the key consideration is the amount of protein needed for egg-laying. In addition, there are also demands for protein for female body maintenance during egg-laying and incubation which may be expected to lead to a loss of endogenous reserves in females that otherwise could be used in egg production. However, a recent study has shown that even under conditions of starvation, apparently only $0.55 \text{ g kg}^{-0.75} \text{ dry protein day}^{-1}$ are lost (Allen & Hume 2001). Hence, protein is mainly needed for clutch production which requires the deposition of relatively large amounts of high-quality protein, especially in birds with a small body mass.

Costs of migratory flight versus egg production

Because there appears to be a strong selection pressure for early laying (Cooke *et al.* 1995, Lepage *et al.* 2000), large birds are likely to utilize residual stores on arrival at the breeding grounds in order to minimise the interval between arrival and egg laying, unless the costs outweigh the benefits. Witter & Cuthill (1993) summarized six potential costs of stores, which fall into the three cost-categories of time, energy (i.e. mass-dependent metabolism, foraging and reproductive costs), and mortality risk (i.e. mass-dependent predation risk, injury risk and pathological costs). In the case of migratory and breeding birds, all these costs may apply. Using allometric equations, Klaassen (2003) evaluated migratory time and energy costs associated with carrying extra stores for breeding in waterfowl where specific data on breeding and migratory ecology were available (see also Nolet 2006). The allometric equation of Norberg (1996) was used to predict flight power requirements, and

it was assumed that after arrival on the breeding grounds, birds require further stores for egg synthesis and catabolism. Both egg production and starvation costs relative to the cost of a migratory flight decrease with an increase in body size. However, the maximal flight range based on Norberg's flight cost equation increases with body size. This implies that only large birds can be expected to use a capital breeding strategy. Furthermore, predictions indicate that larger birds have longer fuelling times than smaller birds in order to meet requirements for egg synthesis, catabolism and migratory flights (Klaassen 2003).

Metabolic processes are slower in large compared to small species, hence the breeding season is extended in large species with longer incubation and chick-rearing periods indicating that large species are time-constrained by the short arctic summer and are more likely to be capital breeders. An important assumption in most models is that energy costs per unit of flight distance increase sharply with an increased fuel load (e.g. Pennycuik 1989, Alerstam & Lindström 1990, Weber *et al.* 1998). An empirical test of this assumption using Knot *Calidris canutus*, showed that transport costs of individuals increased much more than predicted (Kvist *et al.* 2001). The allometric relation linking flight costs (distance over energy) to fuel mass had an exponent of only -0.04 , which contrasts sharply with the predicted exponent of -0.31 based on Pennycuik's equation (1989). Hence, it matters greatly at what distance from the breeding grounds capital stores are acquired.

Body stores and predation risk

The mass of body stores may impair flight performance by increasing wing loading, making a bird more vulnerable to capture by aerial predators (Blem 1975, Lima 1986). Studies of escape responses of birds in relation to body mass when attacked by a simulated predator also indicate that birds suffer an increased predation risk with an increase in mass (Witter *et al.* 1994, Lee *et al.* 1996, Lind *et al.* 1999, Kullberg *et al.* 2000, 2005). Land predators, such as wolves, may pose an important threat to large birds, with poor take-off

abilities, but raptors probably represent the most life-threatening group of predators to birds. Typically, raptors attack birds smaller than themselves, since large prey may be difficult to carry away and larger birds can escape most predators by attaining higher speeds in diving glides (Lima 1993). Waterfowl, with their streamlined bodies and small wings, are suitable for this type of escape behaviour (Hedenström & Rosén 2001, Alerstam 1987). Given the size distribution of birds of prey, predation risk seems to be more of a problem for small (<1 kg) than for large birds. Aside from other reasons, from a predation-risk perspective small birds are likely to opt for an income rather than a capital breeding strategy.

Capital breeding in waders and passerines

Some small passerines arrive at their sub-arctic breeding grounds with residual fat stores (Ojanen 1984, Sandberg 1996, Fransson & Jakobsson 1998), but the stores are a small percentage of total protein and energy costs needed for clutch initiation. The residual stores nevertheless may make the birds less vulnerable to stochasticity in food supply and allow them to lay eggs earlier and dedicate more time to reproduction, instead of foraging. Whether capital breeding occurs in waders, as proposed by Davidson & Evans (1988), has long remained uncertain, largely because of methodological difficulties. Using stable isotope ratios of carbon in eggs, feathers and down, Klaassen *et al.* (2001) investigated the use of nutritional capital in waders breeding throughout the Canadian Arctic and in northeast Greenland. During winter and on migration, the wader species forage on estuarine food sources which have a carbon isotopic signature distinctly higher than that of food ingested on the breeding grounds. The carbon isotope ratios of recently moulted adult feathers collected on the breeding grounds, of which the flight feathers are moulted on the wintering ground and scapular wing feathers en route to the breeding grounds, were much higher than corresponding ratios of juvenile feathers grown on the breeding grounds. Similarly, isotopic signatures of eggs and hatchling down resembled

those of the food ingested on the breeding grounds, clearly showing that the waders are not capital breeders, as proposed by Davidson & Evans (1988). Similar results were obtained by Morrison & Hobson (2004) in a more detailed study of Turnstone *Arenaria interpres* and Knot in the Canadian High Arctic. However, they did find some residual body stores in the earliest clutches. However, these stable isotope studies on waders are in line with size-dependent predictions in protein and energy requirements and predation risks outlined above.

Capital breeding in ducks

The use of exogenous versus endogenous nutrient sources by breeding ducks appears to be extremely diverse, reflecting their broad geographic breeding range, diversity of habitat use, range of foods selected, variation in migration distances and body size (Krapu & Reinecke 1992, Alisauskas & Ankney 1992). Most species eat diets high in invertebrates, especially during the pre-nesting fattening stage, although a few species are more reliant on plant foods (e.g. Canvasback *Aythya americana*, American Wigeon *Anas americana* and Gadwall *A. strepera*). Few arctic duck species have been studied with respect to the capital to income breeding continuum, (all of which have diets containing nearly all animal foods, e.g. marine invertebrates). Common Eider *Somateria mollissima* are the largest arctic duck. They feed intensively immediately before the nesting season, increase 20% in mass and store significant fat and protein reserves to meet the demands of egg production and incubation (Korschgen 1977, Parker & Holm 1990). They do not feed during incubation and may lose up to 45% of their body mass (both protein and lipid reserves) from pre-laying to hatch, similar to the loss in an equivalent sized goose (e.g. Cackling Goose *Branta canadensis minima*, cf. comparison in Ankney 1984), and are generally considered capital breeders. Spectacled Eider *S. fischeri* may use endogenous reserves for egg production, although body mass loss is 26% during incubation. However, they appear less reliant on body reserves than Common Eider during that period, as implied by

lower incubation constancy (90%) and an average of 2.4 recesses per day (1.5 h day^{-1}), during which time some feeding occurs (Flint & Grand 1999). King Eider *S. spectabilis* lose a comparable percentage of body mass during incubation (24%, Kellett & Alisauskas 1997), implying a similar breeding strategy as Spectacled Eider (Krapu & Reinecke 1992). Therefore, these three arctic eider species show differences in the use of body reserves for breeding. The smallest arctic sea duck (Long-tailed Duck *Clangula hyemalis*) has not been investigated. Some species of duck with more temperate ranges, but which also nest at northern latitudes, have been studied. White-winged Scoter *Melanitta fusca* females appear to rely on exogenous resources gathered during pre-laying and laying periods on the nesting grounds in order to meet the costs of both egg production and incubation (Brown & Fredrickson 1987, Krapu & Reinecke 1992). In contrast, Esler & Grand (1994) found that smaller-bodied Pintail females *Anas acuta* nesting in the sub-arctic Yukon-Kuskokwim Delta, Alaska, used lipid reserves for first clutch formation, but not protein or mineral reserves. They also found that lipid reserve use exceeded that needed for clutch formation alone, indicating that, at least partially, maintenance costs were met with stored reserves.

In nearly all these duck species, the capital used during breeding, be it for egg production or incubation, is largely deposited at or in relative proximity to the breeding grounds. This led Owen & Reinecke (1979) to propose four general strategies that waterfowl might use to meet energy requirements for reproduction. What makes these four classes special in the light of many other definitions proposed is the distinction between local and distant capital acquisition namely: (1) reliance on exogenous energy supplemented by small endogenous reserves accumulated *away from* breeding areas, (2) reliance on endogenous energy supplemented by small amounts of exogenous energy accumulated *on* the breeding area, (3) reliance on large endogenous reserves accumulated *away from* the breeding area and (4) reliance on large endogenous energy accumulated *on* (or near) the breeding area.

Thus, arctic and northern ducks exhibit a range of strategies with respect to the use of body stores of fat, protein and minerals, and location of accumulated reserves which reinforces the recognition of a complexity greater than that implied by the simple dichotomy of capital versus income breeding.

Capital breeding in geese and swans

Given their size, this group of birds bears the greatest potential for being distant capital breeders. Although many arctic geese may rely on post-migratory residual body stores to meet nutrient and energetic demands during the early phases of breeding up to the time of hatch (e.g. Ryder 1970, Ankney & MacInnes 1978, McLandress & Raveling 1981, Ankney *et al.* 1991, Spaans *et al.* 1993, Gates *et al.* 1998, Alisauskas & Ankney 1992), many also forage intensively on arrival at the breeding grounds (e.g. Ankney 1977, Budeau *et al.* 1991, Gauthier & Tardif 1991, Bromley & Jarvis 1993, Choinière & Gauthier 1995, Ganter & Cooke 1996, Krapu & Reinecke 1992) indicating that not all geese are strictly capital breeders. In a study of migrating Lesser Snow Goose *Chen caerulescens caerulescens*, Wypkema & Ankney (1979) showed that the fat reserve index of females did not change between staging sites in James Bay and the breeding grounds on the McConnell River, west Hudson Bay, a distance of approximately 1800 km, whereas the protein index increased, indicating that the birds were likely feeding *en route*. Over 60% of the protein needed to meet demands from arrival to hatch was acquired either at the James Bay staging site or between James Bay and McConnell River. Ganter and Cooke (1996) reported that Lesser Snow Goose (female 2.5 kg at the beginning of laying; Ankney & MacInnes 1978) at La Pérouse Bay, Manitoba, appear to be partially income breeders in some years. The larger Greater Snow Goose *Chen caerulescens atlantica* (female 3.1 kg at the beginning of laying), on Bylot Island, Canada, obtains most of its fat and protein requirements for egg production after arrival on the breeding grounds (Choinière & Gauthier 1995, Gauthier *et al.* 2003). Feeding,

therefore, does not appear to be related directly to goose size and even within a species, different patterns of foraging before nesting are evident. Other examples of within-species variation include the brent. The relatively small Dark-bellied Brent Goose *Branta bernicla bernicla* (female 1.4 kg; Cramp & Simmons 1977), breeding in Taimyr, Siberia, which starts laying directly upon arrival at the breeding grounds (Spaans *et al.* 1993). In contrast, Atlantic Brent *Branta bernicla hrota* (female 1.2 kg; Reed *et al.* 1998) laid eggs 10–13 days after arrival on the breeding grounds on Southampton Island, Nunavut, and fed intensively during that period (Ankney 1984). From stable isotope analyses Schmutz *et al.* (2006) conclude that Black Brent *Branta bernicla nigricans* (female 1.0 kg; Reed *et al.* 1998) takes an intermediate position between these two. Cackling Goose (female 1.2 kg; Raveling 1979b) also fed intensively after arrival on the breeding grounds but had insufficient reserves for both egg laying and incubation and needed to feed during the incubation period (Raveling 1979a,b). Dusky Canada Goose *Branta canadensis occidentalis* (female 3.5 kg) fed intensively after arrival on the breeding grounds and acquired up to 66% of the protein required for egg production from foods on the nesting ground (Bromley & Jarvis 1993). Thomas (1983) viewed feeding on the breeding grounds as an extension of migratory hyperphagia, proposing a continuum between two extremes, modified by a variety of factors. In summary, reliance by geese upon stored nutrient reserves is a flexible strategy which is dependent on food quality, its availability to the female at different sites along the migratory route and at breeding grounds, and the cost of spring migration (cf. Choinière & Gauthier 1995).

We made an attempt to explain this apparently large variation in breeding strategies among arctic-breeding waterfowl by collating published and unpublished arrival dates and clutch initiation data for various species and populations of arctic-breeding geese and swans (for data sources see Appendix 1). In general, the further north breeding sites are located, the later birds arrive at the sites (Fig. 1). Although the birds can enjoy light

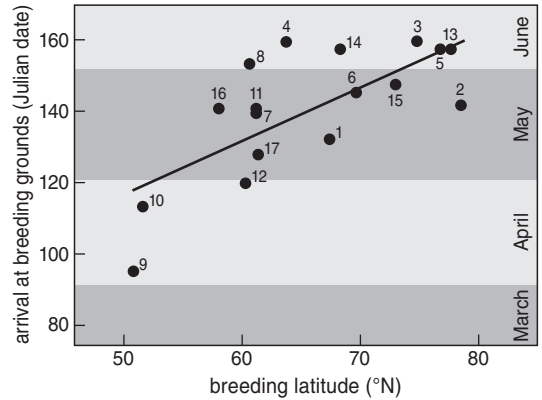


Figure 1. Average arrival date for different species and populations in relation to breeding latitude ($y = 40.9 + 1.511x$, $n = 17$, $R^2 = 0.517$, $P < 0.002$). The numbers with the symbols correspond to the numbers of the studies used in Appendix 1. The further north the location of the breeding grounds the later the birds arrive. At these sites the birds have a short breeding season and they have an increasingly limited time to reproduce successfully at these higher latitudes.

around the clock and at its peak the tundra is a productive environment, the summer season is short in these more northerly locations and the birds are under a severe time constraint. To breed successfully, usually (but not exclusively, e.g. Greater Snow Goose on Bylot Island; Choinière & Gauthier 1995, Gauthier *et al.* 2003) the birds must commence egg-laying soon after arrival (Fig. 2). Rapid follicle maturation takes approximately 14 days in Tundra Swan and 10–12 days in geese (Alisauskas & Ankney 1992) and albumen synthesis takes 1–2 additional days. Romanoff & Romanoff (1949) state that the yolk/follicle contains at least 50% of the egg's protein, indicating that there is a protein demand over the entire period of egg synthesis. When egg laying commences less than 10 days after arrival on the breeding grounds, the production of eggs (at least in part) occurs from residual body stores (area below grey, horizontal line in Fig. 2). The above analysis can be extended to take into account the expected variation in the

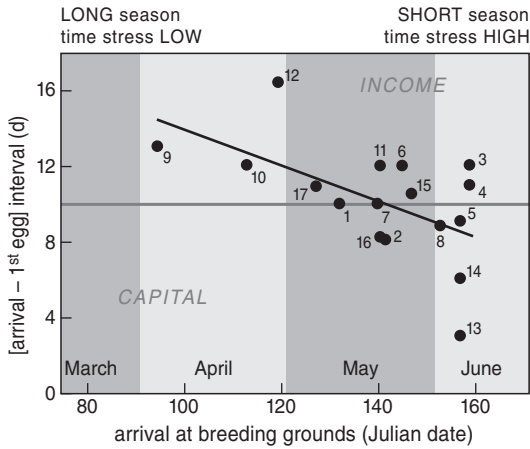


Figure 2. Average interval in days between arrival and clutch initiation for different species and populations of geese and swans in relation to arrival date. Late arrivals at a breeding site are under more time pressure and initiate a clutch sooner upon arrival than birds that arrive at the beginning of the season. The numbers with the symbols correspond to the numbers of the studies used in Appendix 1. Given the time needed for follicle and egg development (see text) these birds are capital breeders, at least in part (area below grey line). The least square regression line is shown ($y = 23.0 - 0.092x$, $n = 17$, $R^2 = 0.316$, $P < 0.02$). The arrival - clutch initiation interval is not entirely independent of arrival date. If arrival date is estimated with error a spurious negative correlation would result. By simulation we estimated that the results depicted here are significant (i.e. $P < 0.05$) as long as we assume the estimated arrival dates in each study to have a 95% confidence interval that is smaller than ± 5 days.

required length of the breeding season for different species, which increases with body size. Thus, large birds tend to arrive on the breeding grounds earlier than small birds (Fig. 3). After correcting for differences in size (by calculating the residual arrival date from Fig. 3), those arriving relatively late are more likely to use endogenous reserves for egg production (Fig. 4).

In addition to the traditional methods for investigation of sources of nutrients for egg production in waterfowl (see Alisauskas & Ankney 1992), the stable isotope method has been applied successfully recently (Gauthier *et al.* 2003,

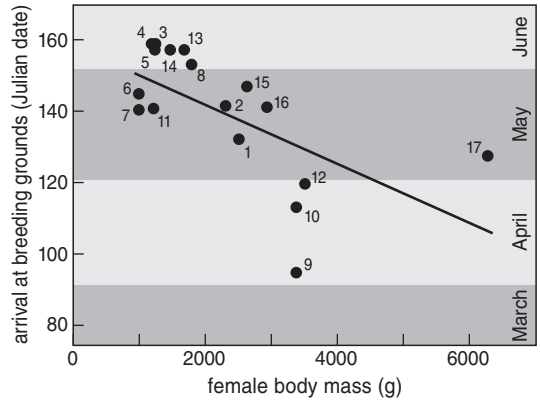


Figure 3. Average arrival date for different species and populations of geese and swans in relation to their body mass ($y = 159.7 - 0.0085x$, $n = 17$, $R^2 = 0.399$, $P < 0.007$). Larger birds need a longer season to reproduce successfully compared with smaller birds and they tend to arrive early on the breeding grounds.

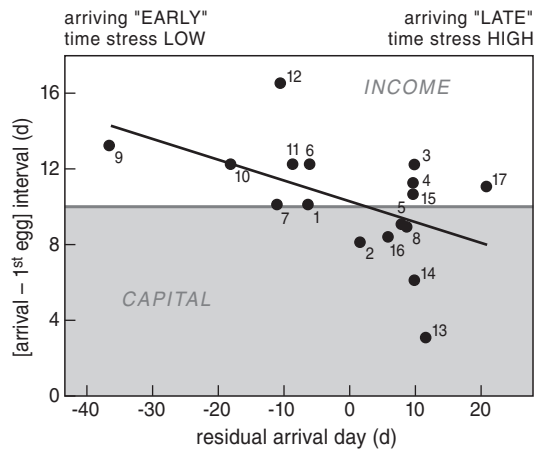


Figure 4. Average arrival - clutch-initiation interval in days for different species and populations of geese and swans in relation to the average arrival date, corrected for female body mass ($y = 10.2 + 0.108x$, $n = 17$, $R^2 = 0.261$, $P < 0.04$). Birds arriving late on the breeding grounds initiate clutches soon after arrival (cf. Fig. 3). Given the time needed for follicle and egg development these birds are capital breeders, at least in part (shaded area).

Schmutz *et al.* 2006, Hobson 2006). We examined inter-annual differences of carbon isotope signatures of Lesser Snow Geese and their eggs from Akimiski Island (Nunavut) in James Bay, Canada. Eggs and down of hatchlings were produced partly from materials incorporated into body stores in regions where maize (corn) or other C_4 plants were growing (Fig. 5). Plants with this type of photosynthesis are absent on Akimiski Island (Blaney & Kotanen 2001). Maize has the C_4 type of photosynthesis and the $\delta^{13}C$ signature of -9 to -14‰ is different from that of a C_3 plant which ranges between -25 (rarely -22) and -35‰ (Ehleringer & Rundel 1988). On occasions between 1997 and 2002, but not every year, the following collections were made: adult feathers from geese feeding in maize fields in spring in Nebraska, down of adults used to line nests on Akimiski Island, down and juvenile feathers collected from the same marked goslings. By analysing carbon isotope ratios in feathers, we attempted to establish the origin of the protein source for egg synthesis, although transfer of carbon from lipid to protein cannot be excluded (Podlesak & McWilliams 2006). Upon arrival at Akimiski Island, Lesser Snow Geese forage on the same plant sources as are available to goslings during the post-hatch period. The interval between peak arrival and peak egg laying was about 10 days in 1998. If Lesser Snow Geese at Akimiski Island were only income breeders, down from hatchlings and juvenile feathers from the same individuals later in the season should show the same carbon isotope signature. However, gosling feathers show a significantly lower $\delta^{13}C$ isotope ratio compared to the down of hatchlings (-26.0 and -23.8‰ , respectively; paired t -test $t = 11.54$, $P < 0.001$, $n = 25$) (Fig. 5). Nevertheless, there is annual variation in the carbon isotope ratios of the hatchling down for 1997 (a late year), 1998 (an early year), and 1999 (an early year) indicating that the dependency of adult females on both lipid and protein body stores derived from C_4 plants varies annually. The carbon isotope ratio of nest down from adult females and feathers from adults that fed in the maize fields of Nebraska clearly

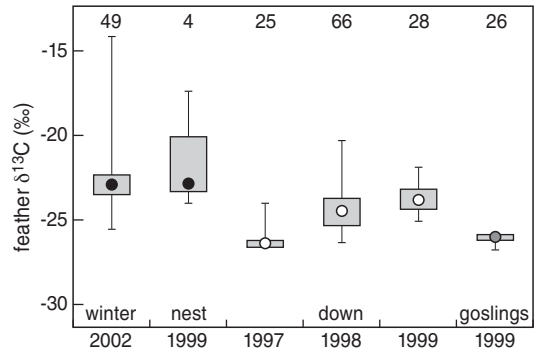


Figure 5. Carbon isotope ratios in feathers from adults, hatchlings and goslings of the Lesser Snow Goose (median, 25 and 75 percentiles, and minimum and maximum are indicated). All material, except the feathers of adults on migration in Nebraska in April 2002, was collected at Akimiski Island (Nunavut) in James Bay. Nest down from adult females was collected in 1999, down from hatchlings was obtained in 1997, 1998 and 1999 and juvenile feathers from goslings were collected in 1999.

indicates that much of the carbon is derived from C_4 sources (cf. Alisauskas *et al.* 1998). It was predicted that eggs laid later might show a more negative $\delta^{13}C$ value than eggs laid earlier, reflecting increased reliance of local C_3 plant sources at the breeding site. In Black Brent, first-laid eggs exhibited slightly higher contributions from endogenous reserves than last-laid eggs (Schmutz *et al.* 2006). However, our Lesser Snow Goose examination of the down isotopic signature among goslings within families indicated similar isotopic ratios, irrespective of hatching order. Similarly, Gauthier *et al.* (2003) found no shift in the isotopic ratio of eggs laid at different times, indicating that reserves formed a constant portion of nutrients placed in eggs over the whole laying period, despite regular feeding at the breeding site. They used the stable isotopes of carbon and nitrogen to determine that the percentage contribution of endogenous reserves to egg protein was only 22% to 33% and to egg lipid was less than 25% in the Greater Snow Goose nesting on Bylot Island. Percentages varied little between years. In Fig. 6 inter-annual varia-

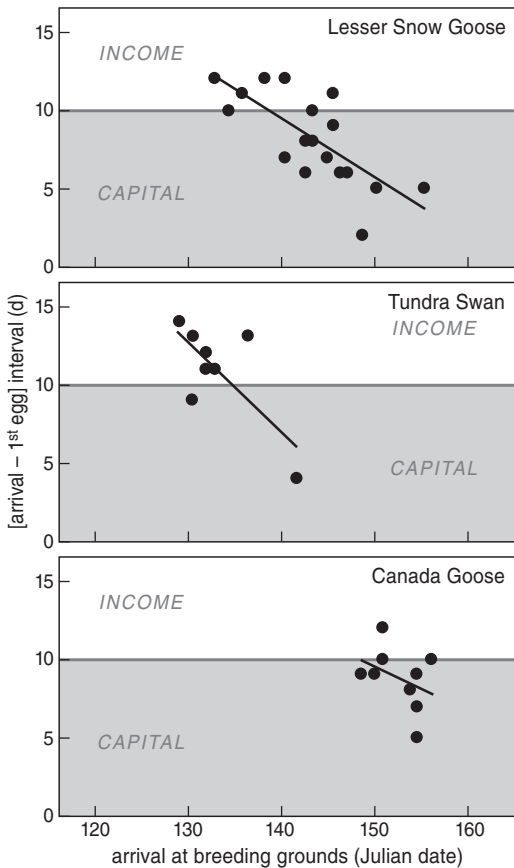


Figure 6. Inter-annual variation in arrival and egg-laying dates at colonies of different species of geese and swans (Lesser Snow Goose *Chen caerulescens caerulescens*, La Pérouse Bay, Manitoba; Canada Goose *Branta canadensis hutchinsii-parvipes*, McConnell River Delta, Nunavut; Tundra Swan *Cygnus columbianus columbianus*, Old Chevak, Alaska). The data also indicate the extent of intra-specific variation in capital breeding in different years (shaded area). Least square regression lines are shown. Lesser Snow Goose: $y = 156.2 - 1.87x$, $n = 19$, $R^2 = 0.523$, $P < 0.001$; Tundra Swan: $y = 64.7 - 0.42x$, $n = 8$, $R^2 = 0.533$, $P < 0.04$; Canada Goose: $y = 41.5 - 0.21x$, $n = 10$, $R^2 = 0.154$, $P = 0.262$. The arrival – clutch initiation interval is not entirely independent of arrival date. If arrival date is estimated with error a spurious negative correlation would result. By simulation we estimated that the results depicted here are significant (i.e. $P < 0.05$) as long as we assume the estimated arrival dates to have a 95% confidence interval that is smaller than ± 7 in Lesser Snow Goose and ± 1.5 days in Tundra Swan.

tion in arrival and egg-laying dates at colonies of different species of geese and swans are shown. For two of the species where the amount of data allows for such an analysis, the results indicate the extent of intra-specific variation in capital breeding in different years.

Conclusion

Capital breeding in arctic birds is not a fixed phenomenon, even in large birds such as geese. It is not widely appreciated that many birds track the receding snow line south of the breeding grounds, but within the Arctic, and feed at coastal and inland sites where sufficient thaw has occurred (Raveling 1979a). At this stage, the migration may be represented as a series of short feeding stops of distances of tens of kilometres rather than hundreds, where *en route* the birds are acquiring resources. Even where birds are flying over seas or oceans to arctic islands, there is a period of feeding on the islands away from the breeding sites (Glahder *et al.* 2006). In fact one of the current uncertainties for some species is the location of birds from the time they leave the established temperate staging sites until their arrival at the nesting sites. Observations indicate that in most cases the birds do not fly directly to the nesting sites. During this period it is known that some species feed intensively on emerging vegetation in the Arctic and sub-Arctic rich in protein and lipid (Krapu & Reinecke 1992). In addition, birds, such as Lesser Snow Goose, are known to eat the remains of egg shells from previous years (Ryder 1969, Gloutney *et al.* 2001) and grub in anaerobic sediment rich in sulphur and microbial products (Handa *et al.* 2002), all of which are requirements for successful egg production. Migration patterns within the Arctic allow the birds to acquire endogenous reserves as little as 10 km from the nesting site (Jefferies *et al.* 2003). Hence, the distinction between capital and income breeding needs further refinement, especially with respect to the geographic origin of the capital.

Differences in regional climate and food availability along the flyways at the different staging sites will affect body store dynamics and hence

breeding strategy. Inter-annual variation in arrival and egg-laying dates indicates intra-specific variation in the extent of capital breeding among years. Waterfowl breeding strategies thus appear to be spatially and temporally flexible at both the species and population levels, so that waterfowl may shift towards income breeding in one year and capital breeding in the next year as circumstances dictate. Body size, foraging patterns, food quality and quantity, and the timing of nesting in relation to seasonal weather events, all contribute to the selection of sites where reserves are acquired by arctic-breeding birds. The use of stable isotopes offers new opportunities to determine the role of endogenous reserves in egg production and incubation in these different scenarios. In addition, it may allow elucidation of the origin of the capital stored, which allows one to distinguish the relative contributions of local capital, distant capital and direct input from nutrients at the breeding sites in reproductive investments.

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SAMENVATTING

De mate waarin trekvogels afhankelijk zijn van overgebleven lichaamsreserves na aankomst in het Arctische broedgebied, is niet voor alle vogels even duidelijk. Het uitgangspunt is veelal dat de korte Arctische zomer de daar broedende vogels onder de nodige tijdsdruk plaatst. Indien trekvogels extra lichaamsreserves mee naar het broedgebied zouden kunnen nemen, zou dit hen in staat stellen om snel na aankomst een begin te maken met de eileg. Zij zouden aldus de tijdsdruk enigszins kunnen beperken en zo hun reproductief succes kunnen verhogen. De hoeveelheid aan extra reserves die meegenomen kan worden, is echter afhankelijk van het lichaamsgewicht, de hogere kosten die het meedragen van deze extra reserves met zich meebrengt, de afstanden die afgelegd moeten worden tussen de pleisterplaatsen langs de trekroute en de plaats van de uiteindelijke bestemming binnen het uitgestrekte broedgebied. Deze afstanden kunnen veel korter zijn dan men voor deze veelal lange-afstandstrekking zou verwachten. Veel vogels kunnen bijvoorbeeld, de wegs meltende sneeuw volgend, op slechts geringe afstand van het uiteindelijke broedgebied nog uitgebreid foerageren. Op regionale of lokale schaal kunnen er dus nog behoorlijk wat reserves worden aangelegd. Het is daarom belangrijk om onderscheid te maken tussen lokaal en ver weg aangelegde reserves. De mate waarin een vogel gebruikmaakt van (lokale dan wel ver weg verkregen) reserves varieert niet alleen tussen soorten, maar ook binnen een soort en blijkt ook van jaar op jaar te kunnen variëren afhankelijk van lokale condities.

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Appendix 1. Sources of data used to generate Figs 1–4 and 6.

Species	Breeding ground	Lat (°N)	Long (°)	Years of study	References
1 <i>Anser albifrons flavirostris</i>	Eqalungmiut Nunat	67.5	-50.5	1979	Fox & Madsen 1981, Cramp & Simmons 1977
2 <i>Anser brachyrynchus</i>	Sassendalen	78.6	17.0	2003–2004	C. Glahder <i>et al.</i> unpubl, Cramp & Simmons 1977
3 <i>Branta bernicla hrota</i>	Bathurst & Seymour Is.	75.0	-100.0	?	Reed <i>et al.</i> 1998
4 <i>Branta bernicla hrota</i>	Southampton Island	64.0	-81.8	?	Reed <i>et al.</i> 1998
5 <i>Branta bernicla hrota</i>	Tusenøyane	77.0	22.0	1991	Madsen <i>et al.</i> 1998, Cramp & Simmons 1977
6 <i>Branta bernicla nigricans</i>	Anderson River	69.7	-128.7	?	Reed <i>et al.</i> 1998
7 <i>Branta bernicla nigricans</i>	Tutakoke River	61.3	-165.6	1987–1993	Lindberg <i>et al.</i> 1997, Reed <i>et al.</i> 1998
8 <i>Branta canadensis hutchinsii-parvipes</i>	McConnell River Delta	60.8	-94.0	1959, 1960, 1964–1971	MacInnes 1962, MacInnes <i>et al.</i> 1974, Dunn & MacInnes 1987
9 <i>Branta canadensis interior</i>	Dog Lake, Manitoba	51.0	-98.0	1954–1955	Klopman 1958, Dunn & MacInnes 1987
10 <i>Branta canadensis interior</i>	Kinoje Lake	51.6	-81.8	1967–1969	Raveling 1978, Dunn & MacInnes 1987
11 <i>Branta canadensis minima</i>	Old Chevak	61.4	-165.4	1971, 1972, 1974	Raveling 1978, Ankney 1984
12 <i>Branta canadensis occidentalis</i>	Copper River Delta	60.4	-145.4	1977–1979	Bromley & Jarvis 1993
13 <i>Branta leucopsis</i>	Diabasøya	77.8	13.8	?	Cramp & Simmons 1977
14 <i>Branta leucopsis</i>	Tobseca	68.6	52.3	2003	G. Eichhorn <i>et al.</i> unpubl, Cramp & Simmons 1977
15 <i>Chen caerulescens atlantica</i>	Bylot Island	73.1	-80.0	1989–1990	Choinière & Gauthier 1995
16 <i>Chen caerulescens caerulescens</i>	La Pérouse Bay	58.1	-94.1	1973–1984 1986–1992	Ganter & Cooke 1996, Ankney & MacInnes 1978
17 <i>Cygnus columbianus columbianus</i>	Old Chevak	61.4	-165.4	1988–1995	Babcock <i>et al.</i> 2002, Limpert & Earnst 1994