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The reliance on distant resources for egg formation in high Arctic breeding barnacle geese *Branta leucopsis*

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Breeding in the high Arctic is time constrained and animals should therefore start with their annual reproduction as early as possible. To allow for such early reproduction in migratory birds, females arrive at the breeding grounds either with body stores or they try to rapidly develop their eggs after arrival using local resources. Svalbard breeding barnacle geese *Branta leucopsis* have to fly non-stop for about 1100 km from their last continental staging site to the archipelago making the transport of body stores costly. However, environmental conditions at the breeding grounds are highly unpredictable favouring residual body stores allowing for egg production after arrival on the breeding grounds. We estimated the reliance on southern continental resources, i.e. body stores for egg formation, in barnacle geese using stable isotope ratios in the geese's forage along the flyway and in their eggs. Females adopted mixed breeding strategies by using southern resources as well as local resources to varying extents for egg formation. Southern capital in lipid-free yolk averaged 41% (range: 23–65%), early laid eggs containing more southern capital than eggs laid late in the season. Yolk lipids and albumen did not vary over time and averaged a southern capital proportion of 54% (range: 32–73%) and 47% (range: 25–88%), respectively. Our findings indicate that female geese vary the use of southern resources when synthesising their eggs and this allocation also varies among egg tissues. Their mixed and flexible use of distant and local resources potentially allows for adaptive adjustments to environmental conditions encountered at the archipelago just before breeding.

How resource allocation contributes to fitness is a key question in life history studies. Birds breeding at high latitudes and wintering in temperate regions are typically confronted with two challenges for reproduction: the right timing of breeding, which includes optimal migration (Alerstam and Lindström 1990), and being physiologically prepared for starting breeding soon after arrival since breeding seasons tend to be short (Perrins 1970, Drent 2006). When migrating northwards, high latitude breeders, like geese, are often incompletely informed about conditions and food availability at the breeding site (e.g. remaining snow cover). However, such information might be crucial for animals relying exclusively on local food resources for maintenance and clutch formation. Since predictability of conditions in distant sites decreases with distance (Bauer et al. 2008), birds that have to cross large ecological barriers before reaching their geographically isolated breeding sites may be especially at risk of mistiming and running into adverse conditions for breeding at their destination.

To deal with such uncertainties, high-latitude breeding birds could opt for building-up body stores at wintering or staging sites, subsequently using these stores for reproduction at the breeding grounds (Drent and Daan 1980, Jonsson 1997). This "capital" breeding strategy guarantees a certain degree of independence from local feeding conditions, allowing for an early start of breeding irrespective of local conditions. However, carrying extra stores might incur substantial time, energy and predation costs (Witter and Cuthill 1993). Additionally, the transport costs of body stores increase with distance (Kvist et al. 2001) and therefore benefits of carrying stores to very distant breeding sites decline (Nolet 2006). However, if the ratio between stores required for reproduction and body size is relatively small the drawbacks can be outbalanced. Therefore, birds with larger body size and comparably small clutches by weight, like Arctic geese, are expected to opt for capital breeding (Klaassen 2003).

Alternatively, birds could arrive at their breeding sites lean, i.e. without the extra-load of stores and rely completely on local food for own maintenance and reproduction. These "income " breeders circumvent the before mentioned costs of carrying stores, but highly depend on favourable feeding conditions in their breeding areas. Therefore, income breeding is likely in species with relatively large clutches and species feeding on readily available resources. However, there is growing evidence from field and modelling data showing capital and income breeding are extremes of a continuum wherein most species follow mixed strategies (Meijer and Drent 1999, Houston et al. 2007).

Given the above mentioned trade offs between the capital and income breeding strategy it is highly conceivable that an individual's position in this capital-income breeding continuum may vary not only in relation to its species-specific size but also in relation to its specific geographic situation (Klaassen et al. 2006). If, for example, a herbivore migrates over land feeding while on migration is usually possible and stores can be built-up very close to the final destination (local capital). In such a case, the difference between capital and income breeding tends to blur. Moreover, some birds respond to variable environmental conditions at staging and breeding sites by adjusting their breeding strategies accordingly (Klaassen et al. 2006), suggesting a certain flexibility in breeding strategies.

For herbivores crossing large distances over sea, feeding en route is impossible. Additionally, feeding conditions at the final destination are difficult to predict from the last staging site before the crossing, all favouring capital breeding.

We investigated variation in the breeding strategy of female barnacle geese from the geographically isolated population at Svalbard. During spring migration, birds cross the Barents Sea during an 1100 km flight before arriving at the archipelago. The predictability of environmental conditions at Svalbard from the last staging site tend to be low (Bauer et al. 2008) and local condition for feeding and nesting, e.g. snow cover, can vary considerably between years (e.g. Prop and de Vries 1993, Madsen et al. 2007). Therefore, the use of endogenous body stores for breeding are expected to be the favoured strategy allowing for an early start of reproduction.

Southern capital, i.e. body stores from continental resources, must be accumulated at staging sites in mid and north Norway at the latest, where geese feed extensively on meadows and agricultural fields (Prop et al. 1998). After arrival at Svalbard, the availability of local resources depends greatly on snow cover (Prop and de Vries 1993), and barnacle geese prefer two main habitat types, the fertilized meadows of pre-breeding sites at the climatically favoured west coast on south-facing mountain slopes below seabird colonies (Prop and de Vries 1993, Hübner 2006) as well as common tundra vegetation in broad valleys (Fox and Bergersen 2005), henceforth referred to as seabird-fertilised tundra and common tundra, respectively.

In our study, we estimated to which extent barnacle geese relied on southern continental and local resources at Svalbard for egg formation using carbon and nitrogen stable isotope ratios in egg tissues and forage. The approach of tracking nutrients to eggs by stable isotopes based on isotopically distinct sources, i.e. food and body stores, allows for quantitative conclusions on nutrient allocation to reproduction (Hobson 2006, 2008). For Svalbard breeding barnacle geese, we expected that (1) females use a considerable amount of southern capital for egg formation to guarantee an early start of breeding. (2) This reliance on southern capital is not expected to vary between years, if conditions at the breeding sites are generally unpredictable. (3) The importance of southern capital for egg formation should decrease in the course of the season as late arriving females may use local resources that become increasingly available as the season progresses.

Methods

Species and population studied

We studied one of the most northerly breeding barnacle goose populations at Breøyane Islands, Kongsfjorden / northern Svalbard (79° 00′N, 12° 04′E) in 2006 and 2007, where about 75 breeding pairs nested at two small islands of less than 1ha (G.W. Gabrielsen and M. J. J. E. Loonen, unpubl.).

Svalbard breeding barnacle geese depart from the wintering site at Solway Firth (GB) at the end of April and first days of May on average (Tombre et al. 2008). Thereafter, the majority of geese spend about two weeks at two main staging areas at Helgeland (mid Norway, 65°N) and Vesterålen (north Norway, 69°N). In the two years of study, in both areas, most geese departed on 17 May in both 2006 and 2007 (Shimmings and Isaksen 2006, 2007, Appendix Fig. 1). After arrival at Svalbard, the majority of barnacle geese typically use the main pre-breeding site at Vårsolbukta (west Spitsbergen, 200 km south of breeding sites) between 20 May and 3 June; but individual staging times are rather short, i.e. 2–3 d (Hübner 2006). Thereafter, barnacle geese are assumed to use several sites for short stopovers while moving north to their breeding grounds (Hübner et al. 2010). They start breeding within 3d after arrival in the breeding areas (Prop and de Vries 1993).

Predictability of environmental conditions at the breeding site

We tested whether geese on spring migration could predict climatic conditions at Svalbard from climatic conditions they encounter at their staging sites in Norway. We used monthly means of air temperature, snow depth and snow cover estimates from 1992 to 2008 recorded at Vega (65° 42′N 11°51′E, mid Norway) and Tromsø (69° 40′N 18° 54′E, north Norway) representative for the Norwegian staging areas and at Longyearbyen (78° 15′N, 15° 28′E) and Hornsund (77° 00′N 15° 30′E, snow depth only) representative for the Svalbard breeding area. Data are provided at www.met.no. We checked for predictability using Pearson correlations; the appropriate period for each site was determined from data of spring migration phenology (Appendix 1, Fig. 1).

Potential resources for egg formation

We used the isotopic composition of goose droppings as proxies for the isotopic composition of goose forage along the flyway. Goose droppings reflect quantitative composition of ingested food (Owen 1975). Additionally, combined measures of nitrogen and carbon stable isotope ratios of forage and droppings of barnacle geese in Russia and the

Netherlands confirmed that isotope ratios in droppings can be used as very reliable proxies of the isotope ratio of the forage (M. Klaassen unpubl.). Fresh droppings (without the whitish uric acid cap) were collected in salt marshes and pastures at Solway Firth, the Scottish wintering sites (first week of May 2006 and 2007, by E. Rees) and at the main staging sites Herøy (mid-Norway) and Vik, Vesterålen (north Norway; second week of May in 2006 and 2007, by P. Shimmings and J. Madsen) to represent southern continental resources. For the pre-breeding period we differentiated between two feeding areas to represent local resources from Svalbard: seabird-fertilised tundra being heavily affected by a marine isotopic signature and common tundra. Seabird-fertilized tundra under bird cliffs is recognized as specific pre-breeding habitat (Hübner et al. 2010), and droppings were collected at Vårsolbukta in May 2005 (by C. Hübner). During the pre-breeding period also common tundra is used for grazing. Droppings from geese feeding on common tundra exclusively were not available. We estimated the isotopic composition of food taken from common tundra vegetation on Svalbard by combining data on diet composition of barnacle geese at Sassendalen (Fox and Bergersen 2005) and isotopic composition of corresponding plant species (Appendix 1, Table 1).

We are aware this may bias to some extent the proportions of the two local food sources for egg formation (based on differences in $\delta^{15}N$) due to isotope-specific digestion in proteins (Sjögersten et al. 2010). However, the proportion of southern continental vs. local sources will not be affected, because the determination bases on differences in $\delta^{13}C$ largely from indigestible fibre (see results).

Analysis of eggs

In June 2006 and 2007, we collected and analysed 95 eggs. In both years, we collected five complete clutches and one randomly selected egg from an additional 25 clutches. Nests for egg collection were selected to guarantee the greatest possible variation in the timing of egg laying using egg density as a proxy of nest initiation date in the field.

All eggs were stored cold and dissected within 3 d after collection. Egg and embryo mass were measured to allow for the calculation of egg laying date following Madsen et al. 2007. Yolk and, if possible, albumen samples were extracted from the eggs and stored in 70% ethanol at −15° C.

The relationship between egg laying date, egg mass and embryo mass (Madsen et al. 2007) was calibrated for barnacle geese using data from 26 eggs with known hatching date (determined by stage of yolk retreat into the embryo's body and cracks on egg shells indicating hatching). In case multiple eggs were collected from the same clutch, the average estimated laying date was calculated. We failed to determine the laying dates of nine eggs due to rotten egg content (2006: 3 eggs, 2007: 6 eggs).

For comparison between years, we calculated relative laying dates by correcting the absolute laying date for the onset of spring. The latter was defined as the first day of a 7 days period with average air temperatures above zero (temperature data from Longyearbyen airport, www.met.no). For 2006 and 2007, this yielded the 22 May (Julian date: 142), and 16 May (Julian date: 136) as the onset of spring, respectively.

Isotope measurements

Droppings were oven-dried at 60° C to constant weight and thereafter ground using an analytical mill with 1mm mesh size. Raw egg tissue, i.e. whole yolk and albumen, were freeze-dried and lipids were removed from a sub-sample of whole yolk by extraction with chloroform-methanol (2/1 by volume). Sub-samples of 200–500 µg of whole yolk, lipid-free yolk, albumen and droppings were analysed for $\delta^{15}N$ (‰ difference from the $^{15}N/^{14}N$ ratio in atmospheric N_2) and for $\delta^{13}C$ (‰ difference from $^{13}C/^{12}C$ ratio in Vienna PeeDee limestone) in a HEKAtech EuroEA elemental analyzer coupled on-line through a Finnigan conflo interface to a Finnigan Delta S isotope ratio mass spectrometer. Reproducibility based on replicate measurements on a casein standard ($n = 145$) during the period of measurements was 0.12‰ (= SD) for $\delta^{15}N$ and 0.21‰ (= SD) for $\delta^{13}C$.

Additionally, $\delta^{13}C$ of yolk lipids was calculated from $\delta^{13}C$ of whole yolk and lipid- free yolk samples and the respective carbon contents of these samples measured simultaneously in the same set-up with $\delta^{13}C$ (see appendix for details). Mean lipid content of dry whole yolk amounted to 59 ± 9.8% ($n = 95$).

In all further analyses we only consider the isotopic composition of lipid-free yolk, albumen and yolk lipids. The abbreviations denote the element and the target tissue, i.e. $\delta^{13}C_{food}$ for carbon isotope ratio of food.

To estimate the proportion of lipid-free yolk, albumen and yolk lipids derived from southern continental versus local resources we used a Bayesian mixing model provided by Semmens and Moore 2008. This statistical approach accounts for uncertainties in isotopic composition of sources and discrimination factors (Table 1). We calculated the median probability that a sample of yolk and albumen originated from three sources (southern continental, fertilised tundra and common tundra) and a yolk lipid sample originated from only two sources (southern continental and Svalbard, since $\delta^{13}C$ signatures from the food sources on the seabird-fertilised tundra and common tundra on Svalbard were indistinguishable; see Results). Herein, we used uninformative priors, i.e. all source contributions are a priori equally likely (Semmens and Moore 2008). For complete clutches, we used the average per nest.

The estimation requires tissue-specific discrimination factors (df, ‰) to account for specific changes in $\delta^{15}N$ and $\delta^{13}C$ (reviewed in: Caut et al. 2009). For lipid-free yolk and albumen originating from southern continental resources, we used dfs of isotopic difference between food taken at the staging site and pectoral muscle of staging geese plus a df for routing of protein from body stores into eggs (Table 1) following the rationale of Gauthier et al. (2003). For lipid-free yolk originating from local resources, dfs were calculated from isotope differences between food at the staging site and yolk stored in follicles during the same period (Table 1). Because there are no data available for

Table 1. Isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of food and tissues of pink-footed geese used for subsequent calculations of discrimination factors (DF) to estimate southern and local resource use for egg formation. Droppings ($n = 44$) were collected at Norwegian staging sites, tissue samples originate from 4 females shot upon arrival at Svalbard. For details on df of albumen see material and methods.

		$\delta^{13}C$, ‰	$\delta^{15}N$, ‰
tissue	Diet Norway	-29.33 ± 0.76	5.37 ± 1.56
	Pectoral muscle (incl. lipids)	-29.21 ± 0.90	6.44 ± 0.52
	Lipid-free yolk	-26.82 ± 0.27	8.15 ± 2.24
	Lipids $_{yolk}$	-32.98 ± 0.54	
Df southern resources	Diet → muscle → lipid-free yolk$^{A, C}$	0.17 ± 1.26	4.60 ± 1.68
	Diet → muscle → albumen $^{A, C}$	0.99 ± 1.29	4.24 ± 1.68
	Diet → body stores → lipids $_{yolk}$ ^{B}	-6.00 ± 1.28	
Df local resources	Diet → lipid-free yolk ^{C}	2.51 ± 0.81	2.78 ± 2.73
	Diet → albumen ^{C}	1.92 ± 0.81	2.06 ± 2.73
	Diet → lipids $_{yolk}$ ^{C}	-3.65 ± 0.56	

A: Df of muscle to egg tissue, i.e. the carnivore model from Hobson (1995), B: assumed, SD = average SD of yolk and albumen, C: SD calculated from original sources.

barnacle geese, we used DFs derived from Svalbard-breeding pink-footed geese *Anser brachyrhynchus* using the same flyway from Norway to Svalbard (Madsen et al. 1999). Droppings for this species were collected in 2004 and 2006 at continental staging sites in Trøndelag (mid Norway) and Vesterålen (north Norway), and processed as described above. Additionally, four female pink-footed geese were shot at Hyttevik, Hornsund (Svalbard) in 2003 immediately after crossing the Barents Sea. From these females, we took yolk samples from well-developed follicles and samples of pectoral muscles, all stored frozen in 70% ethanol before further analysis (see above). Follicles do not contain albumen, so we used DFs for yolk plus the median difference between yolk and albumen in $\delta^{15}N$ (-0.72) and $\delta^{13}C$ (-0.59) found in eggs of mallards *Anas platyrhynchos* ($n = 5$) reared under experimental conditions of isotopically constant diets (Hahn et al unpublished ms) (Table 1).

The df of lipids from southern resources to egg tissue is unknown. Lipid biosynthesis from carbohydrates yields lipids that are depleted by 4 to 8‰ in their $\delta^{13}C$ relative to the carbohydrate source (DeNiro and Epstein 1977). Additionally, we assume that the synthesis of vitellogenin and very low density lipoproteins from body stores in the liver (Speake et al. 1998) also modifies the isotopic composition. We used df $_{lipids}$ of -6.00‰ $\delta^{13}C$, the average of df $_{lipids}$ from local resources (see below), and the df $_{lipids}$ from food to depot fat of -8.00‰ as determined for Yellow-rumped warblers *Dendroica coronata* on a low-protein diet (Podlesak and McWilliams 2007). For df $_{lipids}$ from local resources, we used the isotope difference between food at Norwegian staging sites and yolk lipids extracted from follicles of pink-footed geese, amounting to -3.65‰ (Table 1).

Statistics

We used SPSS 13.0 for calculating basic statistics and R 2.8.0 for linear mixed-effect model calculations (lme4 package, lmer-function). The lmer function does not provide simple significance levels (p-values) because at present it is unclear how to calculate the appropriate degrees of freedom. Therefore, we followed the suggestions of Baayen (2008) and Baayen et al. (2008) and considered factors with absolute t-values > 2 significant at the $p < 0.05$ level. Maternal effects within a clutch were taken into account by grouping dependent data by nest ID. For reduced major axis regressions (RMA) we used software RMA v. 1.17, provided by A.J. Bohonak, San Diego (www.bio.sdsu.edu/pub/andy/rma.html). All data are given as means ± SD if not stated otherwise.

Results

Predictability of environmental conditions

Climatic conditions at the breeding site were not predictable from climatic conditions at both staging sites. Neither temperature nor snow conditions at the mid-Norwegian staging site in April and at departure in May correlated with the actual conditions (May) or future conditions (June) in the breeding area at Svalbard (Table 2). We only found a weak correlation between temperature in May at the north Norwegian staging site and the temperature and snow conditions at the breeding area in the same month (Table 2).

Egg laying

At the breeding site, laying started on 27 May and had ended by 12 June with a median laying date of 1 June (difference between years: $Z = -1.67$, $p = 0.10$, $n = 51$). Consequently, the first eggs were laid about 4.5 weeks after the average departure from the wintering site and ≥ 10 d after the average departure from the Norwegian staging sites (appendix Fig. 1). Median clutch size differed between study years ($Z = -2.87$, $p = 0.004$, $n = 60$) with 4.5 eggs and 4.0 eggs in 2006 and 2007, respectively.

Nitrogen and carbon isotope ratios in food

$\delta^{15}N_{food}$ differed significantly between sites (data log-transformed, $F_{4,74} = 38.78$, $p < 0.001$) and decreased from over-wintering sites in Great Britain to staging sites in Norway, and to Svalbard common tundra (Fig. 1). $\delta^{15}N_{food}$ at the seabird-fertilised tundra was five times higher in comparison to the Norwegian staging site ($t_{46} = -13.2$, $p < 0.001$), or 26 times higher compared to the common tundra food ($t_7 = 18.48$, $p < 0.001$).

Table 2. Pearson correlation statistics between monthly average climatic conditions at the staging site of mid Norway and north Norway and the breeding area at Svalbard during the spring periods from 1992 to 2008. n gives the number of years involved, n/a – not applicable period due either to a later arrival of birds or already complete snow melt.

Staging site		Breeding site		Mid Norway – Svalbard		North Norway – Svalbard		
Parameter	Month	Parameter	Month	R	p	R	p	n
Temperature	April	Temperature	April	0.39	0.12	n/a	17	
			May	0.31	0.22	0.41	0.11	17
			June	0.34	0.19	0.47	0.06	17
		Snow cover	April	−0.53	0.18	n/a	8	
			May	−0.08	0.84	−0.23	0.52	10
		Snow depth	April	−0.35	0.32	n/a	10	
			May	−0.06	0.90	−0.41	0.36	7
	May	Temperature	May	0.30	0.25	0.49	0.05	17
			June	0.27	0.30	0.41	0.11	17
		Snow cover	May	0.01	0.99	−0.11	0.76	10
		Snow depth	May	−0.48	0.27	−0.69	0.09	7
Snow cover	April	Snow cover	April	0.41	0.31	n/a	8	
			May	0.14	0.70	−0.02	0.96	10/7
	May	Snow cover	May	n/a		0.12	0.80	7

Also $\delta^{13}C_{food}$ varied with site ($F_{4,74} = 6.30$, $p < 0.001$, Fig. 2), with higher $\delta^{13}C$ ratios in food from the Svalbard seabird-fertilised tundra compared to the food from the wintering site, and staging sites (Fig. 2) (Bonferroni posthoc test: $p < 0.05$). The common tundra diet had a similar $\delta^{13}C$ ratio as food from the seabird-fertilised tundra ($t = 0.13$, $p = 0.90$), but differed from all southern sites (t-test, all $p < 0.01$, Fig. 1).

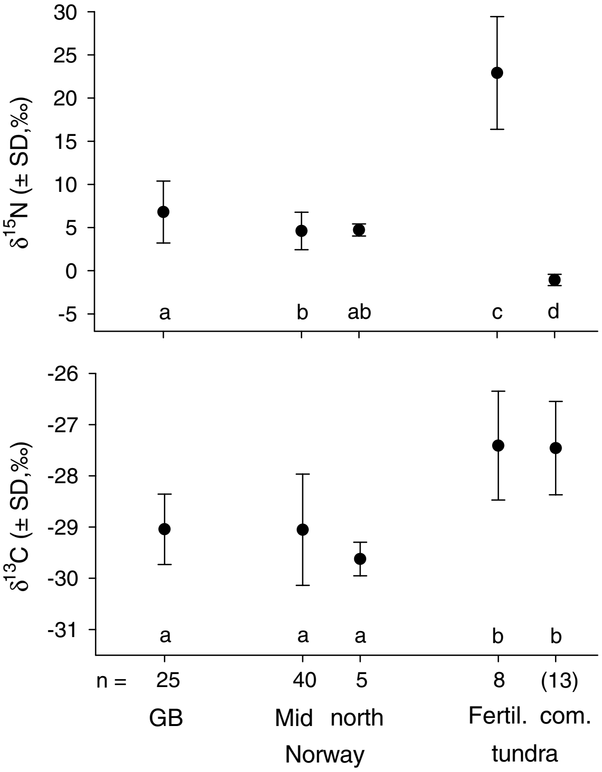

Figure 1. Stable nitrogen isotope ($\delta^{15}N$) and stable carbon isotope ($\delta^{13}C$) composition of droppings along the barnacle goose flyway. Great Britain (GB) and mid and north Norway are the wintering and continental staging sites, respectively. Svalbard resources are presented by droppings from the seabird-fertilised tundra (Fertil) and food from common tundra vegetation (com.). Same letters indicate similar isotopic compositions and n gives samples size per site (for test statistics see results).

Nitrogen and carbon isotope ratios in eggs

There was considerable variation in $\delta^{15}N_{yolk}$ (Fig. 2) ranging from 5.63 to 20.66. Moreover, in 2007, eggs had higher $\delta^{15}N$ values (mean 11.78 ± 3.07‰) than eggs collected in 2006 (mean 9.00 ± 2.32‰; lme: $t = 4.02$, $p < 0.05$). Generally, within-clutch variation of $\delta^{15}N_{yolk}$ was lower than variation between clutches (for complete clutches only: $F_{9,44} = 15.88$, $p < 0.001$). Mean $\delta^{13}C_{yolk}$ amounted to -26.65 ± 0.60‰ (range: -28.04‰ to -25.31‰, Fig. 2), without any difference between years (lme: $t = 0.22$, $p > 0.05$), but larger variation between nests than within nests (for complete clutches only: $F_{9,44} = 17.5$, $p < 0.001$).

$\delta^{15}N_{albumen}$ ranged from 4.80‰ to 15.15‰ with a similar pattern across years as found in lean yolk (lme: $t = 3.79$, $p < 0.05$). Variation in $\delta^{15}N_{albumen}$ between nests was larger as within nests ($F_{3,19} = 5.51$, $p = 0.01$). Additionally, $\delta^{15}N$ of albumen and yolk were related (RMA: $r^2 = 0.82$, with $\delta^{15}N_{albumen} = 0.84 \times \delta^{15}N_{yolk} + 0.66$, $n = 40$). $\delta^{13}C_{albumen}$

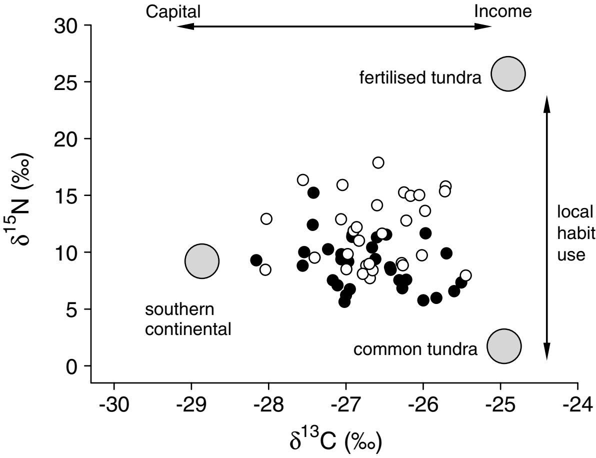

Figure 2. Isotopic triangular space for the estimation of the proportional resource use for formation of lipid-free yolk. Large circles give southern continental and local resources (seabird-fertilised and common tundra) after correction for isotopic discrimination to make these directly comparable to the isotope composition of lipid-free yolk. Samples of lipid-free yolk were collected in 2006 (open circles) and 2007 (filled circles).

averaged $-27.07 \pm 0.68‰$ (difference between years: lme: $t = -0.43$, $p > 0.05$) with a larger variation in $\delta^{13}C$ between nests than within nest (complete clutches only: $F_{3,19} = 11.25$, $p = 0.001$). Albeit less strongly, $\delta^{13}C_{albumen}$ and $\delta^{13}C_{yolk}$ were also related (RMA: $r^2 = 0.45$, $\delta^{13}C_{albumen} = 1.12 \times \delta^{13}C_{yolk} + 2.69$, $n = 40$).

$\delta^{13}C_{lipid}$ varied between $-35.98‰$ and $-31.12‰$ with an overall mean of $-33.32 \pm 0.95‰$ (difference between years: lme: $t = -0.04$, $p > 0.05$). Stable carbon isotope ratios of lipids were positively related to $\delta^{13}C$ in yolk (slope: 1.51, RMA r2 = 0.15) as well as to $\delta^{13}C$ in albumen (slope: 1.27, RMA r2 = 0.15). For nitrogen, there were no relationships between $\delta^{15}N$ of yolk and albumen and egg laying date (Table 3). However, $\delta^{13}C$ in yolk increased significantly with laying date, independently of study year (Table 3). In lipids, $\delta^{13}C$ ratio and laying date were not related (Table 3)

Resource use for egg formation

The proportion of southern continental food used for yolk formation varied between 23 and 65% with an average of 41% (Fig. 3a). Moreover, there was a seasonal decline with highest proportions in early laid eggs/clutches (co-variate laying date: $F_{1,50} = 13.72$, $p < 0.001$, factor year and interaction laying date × year: both $p > 0.50$) (Fig. 3a). The average contribution of local resources to yolk varied between years (for local resources: $F_{1,60} = 15.51$, $p = 0.001$) and was 24% for food from seabird-fertilised tundra and 33% for food from common tundra (Fig. 3a).

In albumen, the average proportion of southern continental resources amounted to 47% (range: 32 to 73%), but did not decrease with laying date ($F_{1,31} = 2.38$, $p = 0.13$; Fig. 3b). The pattern was affected neither by study year nor by their interaction between year and egg laying date (both $p > 0.45$). The average contribution of local resources varied between study years (for local resources: $F_{1,40} = 13.93$, $p = 0.001$), and was 21% for food from the seabird-fertilised tundra and 29% for food from the common tundra (Fig. 3b). Fiftyfour percent of yolk lipids originated from southern continental resources (range: 25–88%), whereas 46% came from local food. The proportion of southern resources in yolk lipids did neither show any pattern according to laying date ($F_{1,46} = 2.35$, $p = 0.13$; Fig. 3c) nor was it different between study years ($F_{1,46} = 0.61$, $p = 0.44$).

Discussion

Using stable isotope ratios in food along the flyway and barnacle goose eggs we revealed a high variability in breeding strategies within a single population. In some females, we found a very high reliance on southern resources whereas in others an almost exclusive use of locally available resources for egg development was found. Although on average the ratio for reliance on southern capital, seabird-fertilised tundra and common tundra resources was approximately 50:20:30, we also found some evidence for egg tissue-specific use of internal reservoirs utilized for formation of yolk, yolk lipids and albumen, and an annually varying importance of the two local habitats on Svalbard for egg formation.

Before we further address the ecological implications of our findings, we briefly discuss the assumptions underlying the isotopic routing of resources to goose eggs. When comparing the isotopic composition of various tissues with the potential resources from which these tissues were synthesized, the elemental composition of the origin and target tissues as well as specific discrimination factors (DF) becomes important (Caut et al. 2009). DFs from a low-lipid low-protein diet, i.e. grass, to egg tissues have not yet been experimentally determined for geese. Consequently, DFs found in experiments with other diets and species are often used (e.g. Gauthier et al. 2003, Schmutz et al. 2006) or DFs derived from precursors of egg tissues, i.e. egg follicles (our approach). DFs for the capital model are difficult to derive, because the isotopic routing from food to stores (protein and lipids) and finally to the egg is not known in detail. We assumed that the formation of body stores and subsequent biosynthesis of different egg tissues from these stores all modify isotopic compositions. We accounted for uncertainty in DF values (Table 1) using Bayesian isotope mixing models (Moore and Semmens 2008), but experimental tests of isotopic routing from body stores to egg tissue are still lacking.

Variability in strategies for egg formation

Large-bodied waterfowl with relatively small clutch volumes, i.e. geese and swans, are promising candidates for capital breeding as they can potentially carry substantial body stores to the breeding grounds for breeding (e.g. for egg formation and own maintenance during incubation) (Klaassen 2003, Drent et al. 2007). By doing so, the animals have the potential for an early start of breeding and are less dependent on the local food availability at the high-latitude breeding site. Hence, females will benefit most from stored resources early in the season, when nutrient and energy requirements are high (Nager 2006), and feeding at high latitude is still restricted by snow cover (Prop and de Vries 1993). Indeed, we here verified in high-Arctic barnacle geese that on average females used 41% to 54%

Table 3. Results of linear mixed models for relationship between $\delta^{15}N$ and $\delta^{13}C$ composition of different egg tissues and laying date, study year and their interaction. Test values >2 are considered statistically significant ($p < 0.05$, see methods for details). Number of eggs and nests within each analysis are given. Asterisks indicate differences at $p > 0.05$ level.

Tissue	Isotope	Laying date	Year	Laying date × year	n_{eggs}	n_{nests}
Lipid-free yolk	$\delta^{15}N$	−1.09	−0.51	1.66	86	51
	$\delta^{13}C$	2.17**	−0.72	0.08		
Albumen	$\delta^{15}N$	0.07	0.45	0.28	46	32
	$\delta^{13}C$	1.49	−0.38	−0.07		
Yolk lipid	$\delta^{13}C$	0.17	−1.01	0.69	79	47

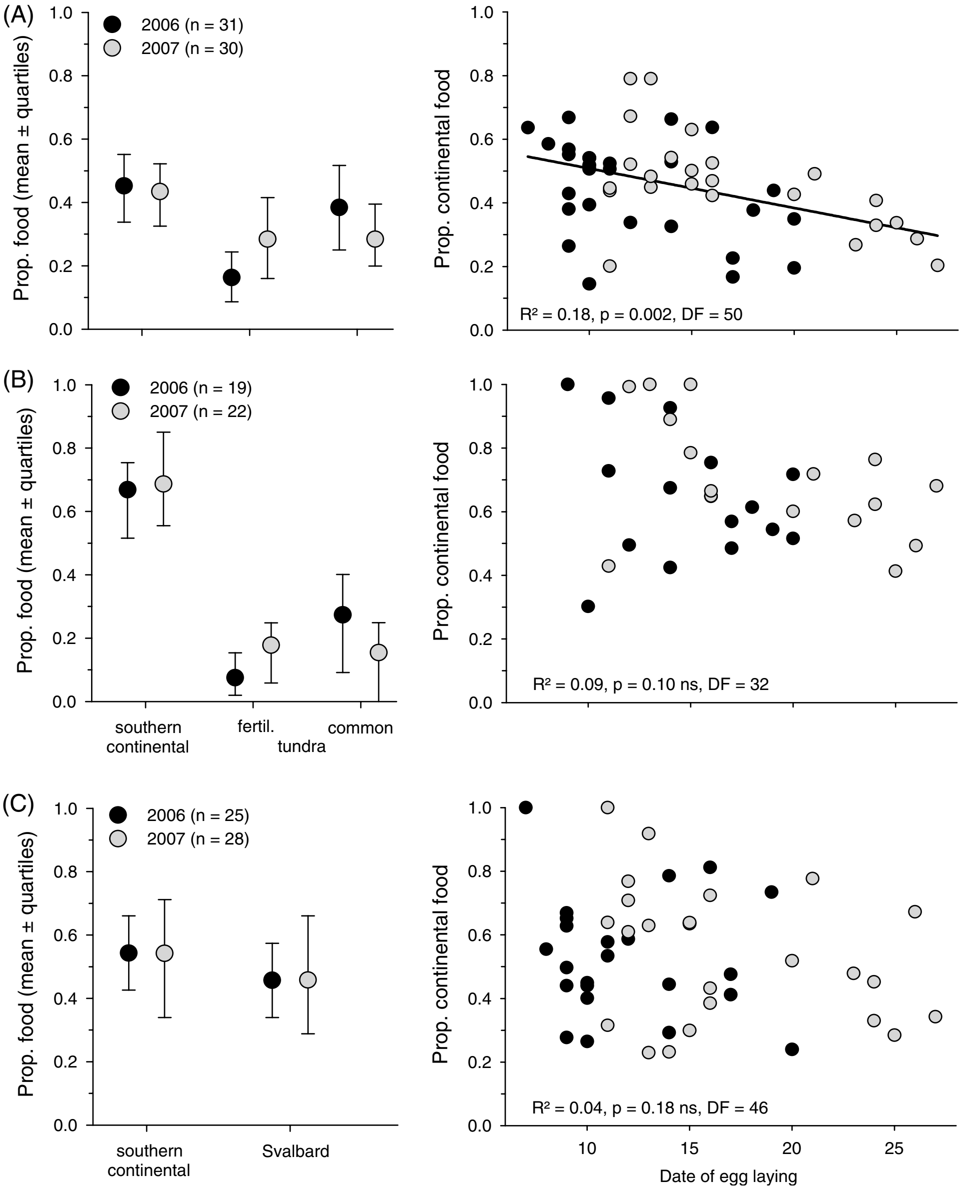

Figure 3. Annual proportion (prop) and temporal pattern of southern continental resources and local resources found in lipid-free yolk (A), albumen (B) and yolk lipids (C) of barnacle goose eggs. Local resources originate from seabird-fertilised and common tundra sites (in lipid-free yolk and albumen) or combined as Svalbard (yolk lipids). The relationship of continental resource use and date of egg laying is given in right column figures. Data are given as means (± quartiles) in left panel and data per female in the right panel. Different years are symbolised with grey and black colour.

of southern capital for egg formation. Such proportions of capital in eggs are among the highest values measured so far (Hobson 2006). Near-comparable reliance on capital for making eggs comes from greater snow geese *Chen caerulescens atlantica*, where Gauthier et al. (2003) verified a portion of 20–33% of endogenous nutrients in eggs. Schmutz et al. (2006) found that brent geese *Branta bernicla* and emperor geese *Anser canagicus* breeding in the same area used about 41% and 55-61% of body stores for yolk formation, respectively. However, in the latter study the use of marine food as "local capital" for yolk formation cannot be excluded, which easily leads to an overestimation of capital use.

What makes our study population special? We argue that the specific isolated geographical position of Svalbard and the local environment at the breeding sites greatly favour capital breeding in barnacle geese at Svalbard and more so than many other Arctic breeding sites for geese. Climate, and therefore the specific vegetation on the archipelago, is typical for the Arctic with a vegetation period of two-three months only and similar to that in other high-Arctic breeding sites. However, what makes the site special is that the Svalbard archipelago is geographically isolated by the Barents Sea, an ecological barrier for herbivorous animals preventing them from feeding during the crossing. Moreover, and potentially more important, geese at their staging sites in Norway cannot predict the actual environmental conditions at Svalbard, at least 1100 km to the north; neither temperature nor snow conditions at the final destination were related to the climatic conditions at the continental staging sites. Thus, when geese depart from Norway they have to consider the risk of encountering adverse conditions at the breeding sites. Consequently, an insurance strategy for early laying would be to carry body stores or precursors of albumen and yolk for egg formation. The benefit for doing so is greatest early in the season, because the availability of local resources improves when the season advances (Prop and de Vries 1993). Accordingly, we found the largest proportion of continental sources in yolk of eggs laid early. In albumen and yolk lipids no seasonal patterns were detectable. This might occur if precursors for these egg tissues can be stored in larger stores over longer times and these stores could be used on demand (Burley and Vadehra 1989). Moreover, the tissue specific proportion of southern resources in the eggs indicated that specific precursors are stored in different tissues or organs, and these stores are used over different times. Therefore, we would expect that tissues formed last, e.g. albumen or the outer part of yolk (e.g. Roudybush et al. 1979), need not necessarily contain the isotope signature of the latest ingested food.

The importance of local pre-breeding habitats for egg formation

Geese departing either early or very late from Norwegian staging sites are in low body condition at departure (Prop et al. 2003). Additionally, early departing females do not necessarily arrive early at the breeding sites; the average time lag between departure from Norway and arrival at the breeding site on Svalbard was approximately 22d (Tombre et al. 1996). Hence, after crossing the Barents Sea, many females use pre-breeding sites at Svalbard to top-up their body stores before egg laying (Hübner 2006). Because geese typically arrive four to six weeks before 50% of the snow has disappeared (Prop and de Vries 1993), birds can forage in certain areas only. The west coast of Svalbard, affected by the warm Gulf current, offers favourable feeding conditions at meadows of south facing seabird-fertilised tundra sites in early spring (Hübner et al. 2010). Resource use for egg formation from seabird-fertilized and common tundra varied annually with a lower contribution from the former in 2006. This potentially indicated lower food availability at these sites at this time, but data on local snow conditions are lacking. From our data it remains unresolved if the use of pre-breeding sites below seabird cliffs is more advantageous for subsequent reproduction than feeding at common tundra sites. Thus, fitness consequences of these individual variations in site use on Svalbard and resource allocation strategies in general (i.e. reliance of income relative to capital) remain to be elucidated.

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Appendix 1

Equation for the estimating of carbon isotope ratio in the lipid fraction of yolk samples from carbon isotope ratio measurements on whole and lipid-free yolk samples

We define:

δC = isotope ratio in the whole (i.e. non-lipid extracted) sample (‰)
δC_l = isotope ratio in the lean fraction of the sample (‰)
δC_f = isotope ratio in the fat fraction of the sample (‰)
c = amount of carbon in the whole (i.e. non-lipid extracted) sample (μgC/μg)
c_l = amount of carbon in the lean fraction of the whole (i.e. non-lipid extracted) sample (μgC/μg)
c_f = amount of carbon in the fat fraction of the whole (i.e. non-lipid extracted) sample (μgC/μg)
M = mass of analysed whole (i.e. non-lipid extracted) sample (μg)
M_l = mass of analysed lean sample (μg)
C = mass of C in whole (i.e. non-lipid extracted) sample analysed (μgC)
C_l = mass of C in lean sample analysed (μgC)
f = fat fraction in the whole (i.e. non-lipid extracted) sample ([mass of whole sample – mass of lean sample]/mass of whole sample)

By definition:

$$\delta C \times c = \delta C_l \times c_l + \delta C_f \times c_f$$

and

$$c = c_l + c_f$$

where

$$c = C/M$$

$$c_l = C_l/[M_l/(1-f)]$$

$$c_f = c - c_l$$

Rearranging and substitution thus yields:

$$\delta C_f = \frac{\delta C \times \dfrac{C}{M} - \delta C_l \dfrac{C_l}{\dfrac{M_l}{1-f}}}{\dfrac{C}{M} - \dfrac{C_l}{\dfrac{M_l}{1-f}}} \quad \text{or}$$

$$\delta C_f = \frac{\delta C \dfrac{C}{M} - \delta C_l \dfrac{C_l(1 - f)}{M_l}}{\dfrac{C}{M} - \dfrac{C_l(1 - f)}{M_l}}$$

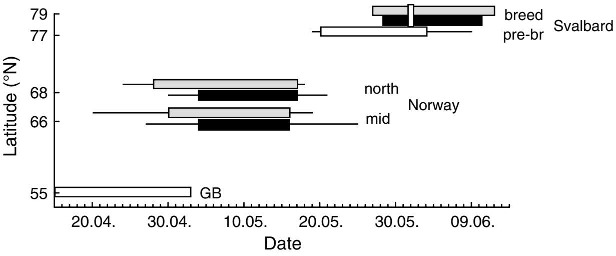

Figure 1. Spring migration phenology and egg laying periods of Svalbard breeding barnacle geese. Bars symbolize the main staging periods (≥ 50% of all birds present), and lines give 25–75% percentiles for the wintering site in Great Britain (GB), the continental staging sites in mid and north Norway, the seabird-fertilised tundra in Vårsolbukta in southern Svalbard (pre-br), and the breeding site in northern Svalbard (breed). Egg laying in Svalbard (79°N) is given as range (first and last date) and median (white bar). Black and grey colours symbolise migration schedule in 2006 and 2007, respectively. For data sources, see Methods.

Table 1. Calculation of isotope composition of bulk diet taken by barnacle geese at the common tundra. Data of the proportion of main diet components are derived from Fox and Bergersen 2005, the corresponding plant species were collected at Sassendalen, Svalbard in June 2005. n gives sample size as well as number of species for each diet component. For the calculation of isotope composition of bulk diet, we assumed equal digestibility in all plants.

Diet components	Percent in diet	δ^{13}C, ‰	SD	δ^{15}N, ‰	SD	n
Grass	8	−27.70	2.30	1.42	3.44	5
Dicots	15	−29.28	1.21	−4.32	0.60	2
Mosses	62	−27.34	2.43	−2.75	2.02	5
Equisetum	15	−26.02		7.82		1
bulk diet (mean)		−27.46	1.56	−1.07	1.33	(13)