The Connectivity of Spring Stopover Sites for Geese Heading to Arctic Breeding Grounds

Authors: Hübner, Christiane E., Tombre, Ingunn M., Griffin, Larry R., Loonen, Maarten J.J.E., Shimmings, Paul, et al.

The connectivity of spring stopover sites for geese heading to arctic breeding grounds

Christiane E. Hübner[1,*], Ingunn M. Tombre[2], Larry R. Griffin[3], Maarten J.J.E. Loonen[4], Paul Shimmings[5] & Ingibjörg S. Jónsdóttir[6]

During the spring migration arctic-breeding geese pause in temperate and sub-arctic staging areas in order to deposit body reserves for breeding. Focusing on a single arctic stopover site in West-Spitsbergen, Svalbard, Norway (Vårsolbukta, 77°45'N, 14°24'E), behavioural strategies of Barnacle Geese *Branta leucopsis* were investigated and body condition and presence of individually marked birds recorded. Individuals using different staging areas earlier along the migration route (Helgeland and Vesterålen on the Norwegian mainland) and heading to different breeding colonies (the close-by Nordenskiöldkysten, and the distant Kongsfjorden) were compared during springs 2003–05. Birds in Vesterålen left the staging area earlier than those in Helgeland, and arrived earlier in Vårsolbukta as well. In Vårsolbukta, females gained body condition at a similar rate regardless of their colony affiliation, whereas males from Nordenskiöldkysten exhibited a smaller overall increase in condition compared to males from Kongsfjorden. The Kongsfjorden birds stayed for a shorter period (average 2.8 days) than those from Nordenskiöldkysten (average 4.0 days). Nordenskiöldkysten birds frequently left Vårsolbukta for short periods presumably visiting the breeding area in order to optimise nest initiation with respect to prevailing snow conditions. The date of final departure was also correlated with nest initiation date at Nordenskiöldkysten. No such relationship for the Kongsfjorden birds was found. We suggest that the geese adopt a 'hopping' strategy, using a network of stopover sites in Svalbard during spring with a last stopover at a buffer area in the proximity to the breeding area. For this vulnerable population it is important to identify the sites forming the links in this chain, and to establish their function and utilisation by geese during the vital pre-breeding period.

Key words: Arctic stopover sites, spring migration, site connectivity, 'hopping' strategy, Barnacle Goose, *Branta leucopsis*

[1]The Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway;
[2]Norwegian Institute for Nature Research, Division of Arctic Ecology, Fram Centre, 9296 Tromsø, Norway; [3]Wildfowl and Wetlands Trust, Eastpark Farm, Caerlaverock, Dumfries, DG14RS, UK; [4]University of Groningen, Arctic Centre, P.O. Box 716, 9700 AS Groningen, The Netherlands; [5]Malvikvegen 811, 7563 Malvik, Norway; [6]Institute of Biology, University of Iceland, Askja, Sturlugata 7, IS-101Reykjavik, Iceland;
*corresponding author (hubner@npolar.no)
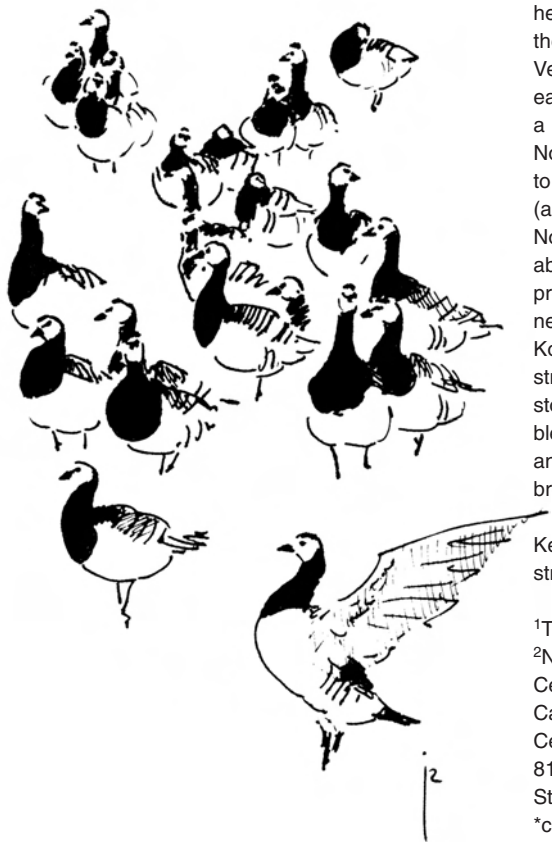
The pre-breeding period plays a decisive role in an animal's life-history, and decisions made during this time have profound effects on subsequent breeding performance (Farmer & Wiens 1998, Madsen 2001, Drent *et al.* 2003). For long-distance migrants, such as arctic-breeding geese, the energetic costs during this period are high since they conduct a resource demanding flight just before embarking on costly breeding activities (Clausen *et al.* 2003, Arzel *et al.* 2006). Snow cover at the breeding location is often still extensive when the birds arrive, resulting in low food availability (Madsen *et al.* 1989, Prop & de Vries 1993). Hence, body reserves

brought to the breeding grounds play an important role in the outcome of reproductive activities, and discrete staging sites along the spring migration route serve to replenish body reserves during the journey north (Gauthier *et al.* 1984, Alerstam & Lindström 1990, Black *et al.* 1991, Warnock & Bishop 1998, Madsen 2001, Tombre *et al.* 2008).

In addition to the food obtained at the staging areas (Black *et al.* 1991, Ebbinge & Spaans 1995, Prop *et al.* 2003) arctic geese supplement their body reserves by continuing to feed on the breeding grounds prior to egg-laying (Prop *et al.* 1984, Choinière & Gauthier 1995, Hübner 2006). Geese breeding in Svalbard travel over 1,000 km over the open sea during migration (Madsen *et al.* 1999, Fig. 1). After arrival they congregate in vegetated areas with advanced snow melt in order to regain fat reserves before the final move to the breeding areas (Prop & de Vries 1993, Mehlum 1998, Hübner 2006). Satellite tracking studies have proven successful in locating pre-breeding areas in the Arctic (e.g. Clausen *et al.* 2003, Griffin 2008). Subsequent direct observations can determine the importance of these sites. However, detailed studies are rare and little is known about the utilization and function of these sites at present.

The reproductive success of a migrating goose depends on an early arrival at the breeding location and is positively correlated with the body reserves (Ankney & MacInnes 1978, Prop & de Vries 1993, Dalhaug *et al.* 1996). The optimal strategy at a stopover site will therefore depend on the date in relation to the progress of snow melt, the bird's body condition and the distance remaining to its ultimate destination. On migration north from the UK wintering areas, the Svalbard-breeding population of the Barnacle Goose *Branta leucopsis* utilise staging sites in Helgeland, central Norway (Fig. 1), and Vesterålen in northern Norway (Follestad & Shimmings 2001, Tombre *et al.* 2005). The distance of approximately 300 km between these staging sites has the potential to influence body reserve dynamics and the timing of arrival and further migratory steps within Svalbard. Once in Svalbard, the distance to their breeding colonies differs considerably which presumably will be reflected in their behavioural decisions at the pre-breeding sites.

In the present study, the connectivity of stopover sites during the spring migration of Barnacle Geese is examined, with a special emphasis on the pre-breeding site at Vårsolbukta on the west coast of Svalbard. Here, the body condition and timing decisions of individually marked geese were recorded. Vårsolbukta is visited by approximately 20% of the entire Svalbard population during the pre-breeding period (Hübner 2006). The geese are able to supplement fat reserves during their stay, but variation in body reserve gain among individuals is high (Hübner 2006). This study provides a unique opportunity to evaluate the utilisation of an arctic pre-breeding site by geese coming from different spring staging sites and with different breeding colony affiliations. Such a site is expected to have different functions for different individuals, depending on the distance from the previous site and the distance to the final destination.

METHODS

Study area

Vårsolbukta (77°45'N, 14°24'E, Fig. 1) is characterised by an early snow melt due to its south-westerly-facing slopes and relatively rich vegetation fertilized by a large seabird colony (for details see Hübner 2006). Consequently, it is an attractive feeding area for geese during spring when food availability in Svalbard is limited. Observations were conducted in a 4.5 km² study area that covered most of the favourable feeding habitat during 2003–05. Alongside the large numbers of Barnacle Geese using Vårsolbukta in early spring, are Pink-footed Geese *Anser brachyrhynchus* and Light-bellied Brent Geese *Branta hrota* with maximum daily counts of 2042, 1003, and 253, respectively, during the study period (Hübner 2007).

For a description of the Norwegian staging areas, Helgeland and Vesterålen, see Prop *et al.* (2003) and Tombre *et al.* (2005, 2008, 2009). For the breeding colonies in Svalbard, Nordenskiöldkysten and Kongsfjorden, see Prop & de Vries (1993) and Loonen (1997).

Study species

During the study, the Svalbard Barnacle Goose population was estimated to be 25,000 individuals (WWT, unpubl. data). The main wintering area of the population is on the Solway Firth, UK (55°N, 03°W, Fig. 1). Spring migration commences in mid-April. On their way north, the geese stage on the coastal islands of Helgeland, mid-Norway (65°N, 12°E) and Vesterålen in northern Norway (69°N, 16°E), until the last week of May. Barnacle Geese breed in colonies or loose groups mainly along the west coast of Spitsbergen between 76°35'N and 79°50'N (Mehlum 1998) and egg-laying commences at the beginning of June, shortly after nest sites become snow free (Madsen *et al.* 2007).
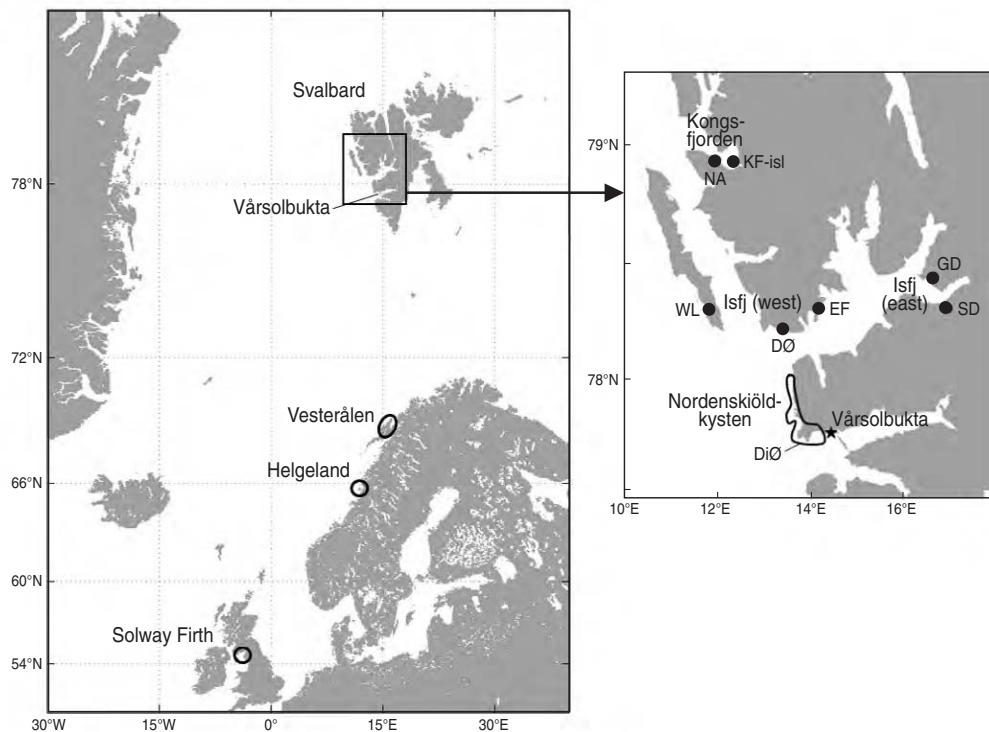
Figure 1. Flyway of the Svalbard Barnacle Goose: wintering area in UK (Solway Firth), staging areas in Norway (Helgeland and Vesterålen), a stopover site in Svalbard (Vårsolbukta) and breeding colonies; NA = Ny-Ålesund, KF-isl = islands in Kongsfjorden, Isfj = Isfjorden, WL = Wilson laguna, DØ = Daudmannsøyra, EF = Erdmannflya, GD = Gipsdalen, SD = Sassendalen, DiØ = Diabasøya.

Ring resighting

Geese have been caught and marked in several breeding colonies since the 1970s, and at the time of this study about 8% of the population was ringed with individual alphanumeric coded leg-rings. Rings can be identified through a telescope (with a 20–60× zoom) up to 250 m (occasionally a 135× magnification was used to read rings up to 700 m). To avoid pseudo-replication in analyses concerning the timing of migration, marked pairs were regarded as a single datum point.

Norwegian staging areas – Goose flocks were systematically observed and rings recorded on a daily basis from roads and other vantage points at a few key sites. To estimate departure dates, last sightings of marked individuals were used. These were inevitably biased towards earlier dates if individuals are missed while still present in an area. However, such a bias will presumably be similar in all areas, allowing us to compare departure dates from different areas.

Vårsolbukta – The area was scanned daily for ringed birds, from 16 May to 9 June each year, which included the full goose staging period. Where possible the ring codes were identified and the sex was determined.

Colony affiliation

Assuming that the geese ringed in an area are affiliated to that area in later years (due to their high fidelity to breeding and moulting sites, Black *et al.* 2007), marked Barnacle Geese were associated with a specific breeding colony. The ringing locations in Svalbard were pooled into breeding area categories, hereafter referred to as colonies, according to their distance and direction from the study area (Fig. 1): (1) Nordenskiöldkysten: including all ringing locations along the west coast of Nordenskiöldland (3–35 km, "local"); (2) Kongsfjorden: the islands in Kongsfjorden and the settlement of Ny-Ålesund (140–145 km, "distant"); (3) Isfjorden (west): Daudmannsøyra, Prins Karls Forland (Wilson laguna) and Erdmannflya (50–85 km); (4) Isfjorden (east): Sassendalen and Gipsdalen (80–95 km). The number of ringed birds differs between colonies and changes between years due to mortality and differential ringing efforts. As not all of the colonies were visited frequently, ring sighting data from the wintering area were used to estimate the total number of rings in each colony per year. These yearly estimates were then used to calculate the proportions of ringed birds per colony seen in

Vårsolbukta during the three years. The number of years a bird was seen in Vårsolbukta was tallied in order to estimate site fidelity between years for individuals from the two colonies for which most data were available (Nordenskiöldkysten and Kongsfjorden). For this purpose, we only used birds that were recorded in Vårsolbukta in 2005 and ringed before 2003 to avoid any bias due to mortality or new rings being added to the population during the study period.

Body condition

Body condition of ringed individuals was assessed by the use of an abdominal profile (AP) index (Owen 1981), a subjective estimate of body condition in geese. The index exhibits a linear relation to body mass or fat reserves (Fox *et al.* 1998, Madsen & Klaassen 2006). Total AP gain was calculated by subtracting the AP at first sighting from the AP at last sighting. Only birds staying longer than 24 hours were included in the analyses of AP gain.

Time of nest initiation

The island of Diabas at Nordenskiöldkysten (77°50'N, 13°45'E; linear distance from Vårsolbukta: c. 16 km; Fig. 1) was monitored during the nesting period of 2004 from arrival at the colony through to the end of the incubation with nest initiation dates being recorded. At Ny-Ålesund, Kongsfjorden (78°55'N, 11°56'E; Fig. 1) in 2003 and 2005, detailed observations started at the end of June, and breeding phenology is thus based on hatch dates. Hatch dates of families with at least one ringed parent were established during nest checks or by backdating using an estimate of gosling age at first sighting (Larsson & Forslund 1991). Nest initiation dates were estimated from hatch dates by subtracting the average length of the incubation period (24 days) and the number of days corresponding to the clutch size or family size at first sighting.

Statistical analyses

Except for the Capture–Mark–Recapture (CMR) modelling, all statistical tests were carried out using the statistical software R, version 2.2.1 (R Development Core Team 2005). To test for segregation of birds with different colony affiliation at the staging areas in Norway a general linear mixed model was used, with colony affiliation as response variable, staging areas as fixed factor and repeated measures of individual rings over successive years. To test for colony differences in fidelity to the arctic stopover site at Vårsolbukta, a contingency table test (χ^2, columns: colonies; rows: the number of years a bird was seen) was performed. Linear models

were used to examine AP at arrival at Vårsolbukta (for each sex separately; predictor variables: $date_{arrival}$ and staging area), AP gain during the stay in Vårsolbukta (for each sex separately; predictor variables: $AP_{arrival}$, colony affiliation, $date_{arrival}$ and stopover duration), departure date from staging sites in Norway (predictor variable: staging area), date of arrival in Vårsolbukta (predictor variable: staging area and colony affiliation), time elapsed between departure from the staging sites and arrival in Vårsolbukta (predictor variable: staging area) and nest initiation (predictor variable: $date_{departure}$). Non-significant variables were removed from the models by stepwise iteration. In all analyses, year was included as predictor variable to control for year effects.

CMR analyses (Lebreton *et al.* 1992) were used to calculate emigration Φ, immigration γ and resighting probabilities p_r for ringed individuals at Vårsolbukta (Schaub *et al.* 2001, Verkuil *et al.* 2010). Mortality during the short stopover stays of migration is negligible and true survival is assumed to be one (Schaub *et al.* 2001). Cormack–Jolly–Seber models within the program MARK 4.3 (White & Burnham 1999) were used to separate emigration (and immigration) probability from resighting probability. The fit of the general model to the data set was tested with the bootstrap goodness-of-fit test provided by MARK (Cooch & White 2006) and the most parsimonious model was selected based on Akaike's Information Criterion (AIC).

Individual sighting histories were established for birds observed between 16 May and 9 June in each year. The daily records were pooled into seven time periods of three days (t) and an initial four day period. Each vector was assigned to one of six groups that represented the six combinations of years (2003, 2004 and 2005) and colony affiliations (col: Nordenskiöldkysten (NK) and Kongsfjorden (KF)), i.e. NK-2003, KF-2003, etc. Thus, the general model was: Φ (year×col×t), p_r(year×col×t) and it was possible to test for differences between years, breeding colonies and their interactions. Including t in the model allowed for the identification of possible time dependencies (Lebreton *et al.* 1992).

In addition, the mean stopover duration (S) of birds seen during each time period was calculated (Schaub *et al.* 2001). S is the sum of S_b and S_a, with S_b and S_a being the estimated stopover duration before and after the time period, respectively. Since most birds had left the study area after the last time period, Φ_{n+1} was set equal to Φ_n, with n being the number of time periods. Likewise, no geese were seen before the first occasion and $\gamma_{n+1} = \gamma_n$.

Arrival and departure dates are based on first and last sightings of ringed birds in the study area. All dates are presented as day numbers starting from May, i.e. 1 = 1 May, 2 = 2 May, etc.

RESULTS

Use of stopover sites
Norwegian staging areas – In Vesterålen, 92.9% of the individuals observed over the years ($n = 28$) were affiliated to the Kongsfjorden breeding colony, whereas for Helgeland this number was only 61.6% ($n = 109$; GLMM over the complete data set with observations for three years, $F_{1,204} = 12.95$, $P < 0.001$). Only 6 Kongsfjorden birds were observed in both staging areas in the same or in consecutive years.

Vårsolbukta – Totals of 241, 168 and 230 ringed Barnacle Geese with known colony affiliations were observed in Vårsolbukta during 2003, 2004 and 2005, respectively. The proportion of birds from the Nordenskiöldkysten colony that used Vårsolbukta was 2–8 times larger than the proportions of birds from other colonies (Fig. 2). Most of the ringed birds visited Vårsolbukta in one year only (Nordenskiöldkysten: 43%, Kongsfjorden: 74%), which indicates alternative stopover sites are available. Relatively more birds from Nordenskiöldkysten were seen in two or three of the years (41 and 16%) compared to birds breeding in Kongsfjorden (22 and 4%; $\chi^2_2 = 7.51$, $P < 0.05$, $n = 56$ and 27 for Nordenskiöldkysten and Kongsfjorden birds, respectively).
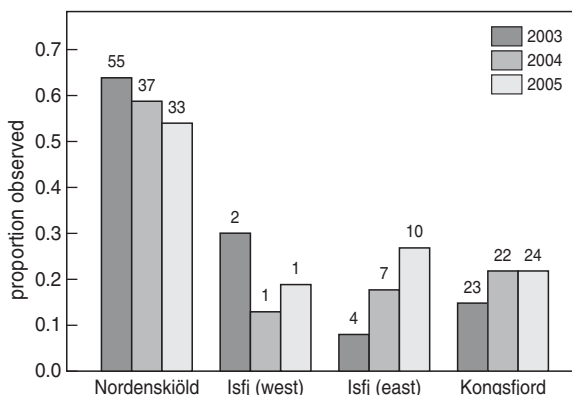
Figure 2. Proportions of all ringed birds per colony that were seen in Vårsolbukta, Svalbard, for four Barnacle Goose colony areas in Svalbard (Fig. 1), during spring 2003, 2004 and 2005. Isfj = Isfjorden. Numbers over columns are the number of geese seen in Vårsolbukta.

Body condition dynamics
Female AP at arrival was positively correlated with arrival date (ANCOVA, $F_{1,230} = 31.9$, $P < 0.001$, predicted regression coefficient B = 0.07), i.e. late arriving females had larger fat reserves than those arriving early. Male AP at arrival in Vårsolbukta was independent of arrival date (ANCOVA, $F_{1,253} = 0.7$, $P = 0.4$). In neither sex did AP at arrival differ between birds from different staging areas (females: $F_{1,20} = 0.0$, $P = 0.98$; males: $F_{1,20} = 0.2$, $P = 0.6$).

Female gain in fat reserves showed a negative relationship to AP at arrival in Vårsolbukta (ANCOVA, $F_{1,123} = 26.6$, $P < 0.001$, B = –0.42), i.e. females in poor body condition gained more fat reserves than those arriving in better condition. There was no difference in AP gain between females from different colonies ($F_{1,119} = 1.8$, $P = 0.2$) and AP gain was independent of arrival date ($F_{1,119} = 0.0$, $P = 0.9$).

Males heading towards Nordenskiöldkysten gained less AP units during their stay in Vårsolbukta (mean = 0.1 ± 0.06 (SE), $n = 87$), compared to Kongsfjorden males (mean = 0.5 ± 0.07, $n = 40$, ANCOVA, $F_{1,120} = 11.3$, $P < 0.01$). Male AP gain decreased with increasing AP at arrival in Vårsolbukta ($F_{1,120} = 50.1$, $P < 0.001$, B = –0.81). Arrival date in Vårsolbukta did not show a significant effect on AP gain ($F_{1,120} = 3.6$, $P = 0.06$, B = –0.03). Adding stopover duration did not improve any of the models above (for all models: ns).

Timing of movements
The mean date of last sighting of ringed birds in Norway differed between staging areas (Helgeland: mean = 15.5 ± 0.2, $n = 278$; Vesterålen: mean = 12.0 ± 0.6, $n = 83$; ANOVA, $F_{1,355} = 51.79$, $P < 0.001$). Birds staging in Helgeland arrived later in Vårsolbukta than birds staging in Vesterålen (Helgeland: mean = 27.3 ± 0.6, $n = 34$; Vesterålen: mean = 22.8 ± 1.8, $n = 8$; ANOVA, $F_{1,40} = 8.53$, $P < 0.01$). The mean time elapsed between the last sighting in Norway and the first sighting in Vårsolbukta was similar for individuals staging in the two mainland staging areas (Helgeland: mean = 12.7 d (range: 3–28 d), $n = 34$; Vesterålen: mean = 11.9 d (range: 5–17 d), $n = 8$; ANOVA, $F_{1,40} = 0.17$, $P = 0.7$). There was no difference in the date of first sighting in Vårsolbukta for birds with different breeding colony affiliation (ANOVA, $F_{1,263} = 2.67$, $P = 0.1$).

The goodness-of-fit-test for the general CMR-model was not significant for immigration ($\hat{c} = 1.06$, $P = 0.27$) and emigration ($\hat{c} = 1.04$, $P = 0.35$), implying that the model assumptions were met. Testing the set of models revealed that both immigration and emigration
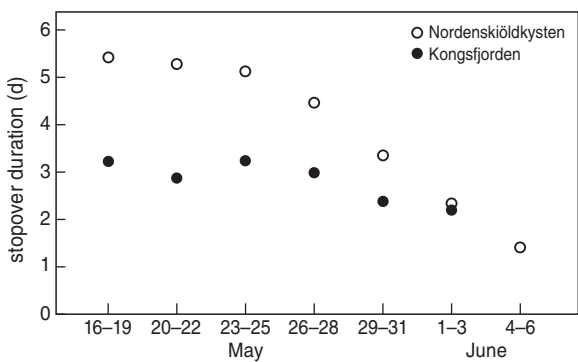
Figure 3. Mean length of stay by Barnacle Geese in the stopover area Vårsolbukta breeding in Nordenskiöldkysten and Kongsfjorden based on CMR-analyses. Three years pooled (2003–05). Days were pooled in periods of three or four days. Stopover duration by Kongsfjorden birds in the seventh period could not be calculated due to limited sample size.

were related to colony and time period, whereas resighting probability was related to colony alone (Table 1). The most parsimonious models did not include year thus indicating no year differences.

Birds from Nordenskiöldkysten stayed longer than birds from Kongsfjorden and length of stay generally decreased with progressing season (Nordenskiöldkysten: mean = 4.0 ± 0.3 d, Kongsfjorden: mean = 2.8 ± 0.1 d, Fig. 3). Resighting probability was lower for birds from the local breeding area Nordenskiöldkysten ($p_r = 0.55 \pm 0.05$) compared to birds from Kongsfjorden ($p_r = 0.94 \pm 0.06$). This difference indicates that local birds more frequently left the study area for one or several days returning afterwards.

Table 1. The three most parsimonious models for immigration γ, emigration Φ and resighting probability p_r for Barnacle Geese in Vårsolbukta, Svalbard, during springs 2003–05, ordered by Akaike's Information Criterion (AIC_c). ΔAIC_c = difference in AIC compared to the most parsimonious model; AIC_c weight = measure of model selection certainty; NP = number of parameters; col = breeding colony affiliation (Nordenskiöldkysten or Kongsfjorden); t = time period (3 (4) days pooled).

Model	AIC_c	ΔAIC_c	AIC_c weight	NP
Immigration				
γ (col×t), p_r(col)	833.06	0	0.9927	15
γ (col), p_r(col×t)	842.91	9.86	0.0072	15
γ (col×t), p_r(col×t)	848.03	14.97	0.0006	24
Emigration				
Φ (col×t), p_r(col)	841.84	0	0.9194	15
Φ (col), p_r(col×t)	848.74	6.90	0.0292	16
Φ (col), p_r(t)	848.81	6.98	0.0281	9

Timing of breeding

Nordenskiöldkysten – There was a positive relationship between last sighting date in Vårsolbukta and nest initiation date (linear regression, $R^2 = 0.65$, $P < 0.01$, $n = 10$), with a mean time period elapsed between sightings in the two areas of 5.2 d (range: 2–8 d; Fig. 4A).

Kongsfjorden – We found no relationship between nest initiation date and date of last sighting in Vårsolbukta ($R^2 = 0.1$, $P > 0.4$, $n = 15$). The mean time elapsed between the two sightings was 12.0 d (range: 7–26 d, $n = 15$; Fig. 4B).

DISCUSSION

During the three years of the study, the arctic stopover site of Vårsolbukta was used by geese from many different colonies. Local birds from nearby Nordenskiöldkysten used the area more extensively and showed a higher site fidelity in consecutive years than birds from the distant breeding area of Kongsfjorden, indicating a differential utilisation pattern of stopover sites depending on the birds' stage of migration.

At the staging areas in Norway, a partial segregation of birds from different colonies could be seen. Relatively more individuals breeding at Kongsfjorden, opposed to geese heading to the Nordenskiöldkysten colony, were observed in the staging area of Vesterålen, whereas this number was more equal in the staging area of Helgeland. The observation that geese in Vesterålen leave c. 3 days earlier than those staging in Helgeland, despite being closer to the breeding grounds, indicates that feeding conditions may have allowed for more rapid fattening in Vesterålen. The earlier departure from Vesterålen was also reflected in an earlier arrival in Vårsolbukta. For the geese breeding in the Kongsfjorden area, the saving in time and energy is advantageous since they have to travel a further c. 140 km to reach their breeding colony.

Performance during stopover in Svalbard

Alerstam & Lindström (1990) state that the most important selective forces during migration are time, body reserves and predation. Geese that still have to cover a long distance to their breeding areas experience a stronger time pressure during stopover at a given site and date than birds that breed in proximity to it. In our study, geese breeding in Kongsfjorden had a shorter stay in Vårsolbukta than the local breeders from Nordenskiöldkysten and generally spent their entire stopover time feeding in the area. Nordenskiöldkysten birds, on the other hand, stayed longer and left the area
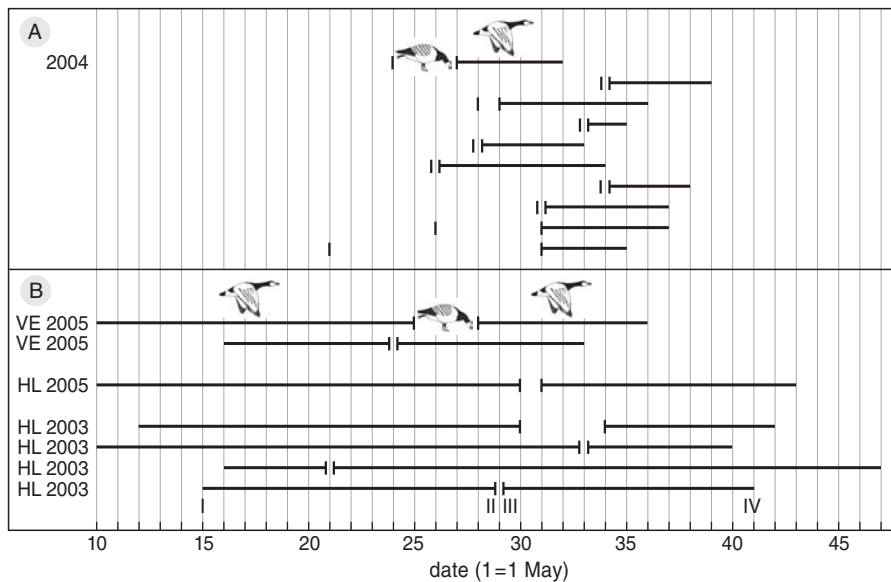
Figure 4. Estimated migration schedules of individual Barnacle Geese (for geographical details see Fig. 1). (A) Individuals breeding at Nordenskiöldkysten in 2004; note that none of the birds were seen in the Norwegian staging areas; (B) Individuals breeding in Kongsfjorden area in 2003 and 2005; VE: staging in Vesterålen; HL: staging in Helgeland. Lines depict the time used for migratory flights; I = date of last sighting in the Norwegian staging area; II = date of first sighting in Vårsolbukta; III = date of last sighting in Vårsolbukta; IV = date of nest initiation.

more frequently. We suspect that they visited their breeding colony during these absences, as individuals may compete for the best nest sites and an early arrival at the breeding location is thus advantageous (Prop *et al.* 1984, Alsos *et al.* 1998). However, if snow conditions still prevent settling and limit food access, waiting in the breeding area would result in high energy expenditure (Drent *et al.* 2003). Being able to return to a site close by, where food availability has been sampled earlier and proven sufficient, allows the geese to check conditions at the breeding locations without risking a decline of body condition.

Length of stay in our stopover site was considerably shorter than in the Norwegian staging areas, where the geese spend on average 11 days (Prop *et al.* 2003). Lyons & Haig (1995) found that the speed of migration of shorebirds increased when the birds approached their ultimate destination. It seems that Barnacle Geese also speed up their migration once in Svalbard. Stopover time additionally decreased with the progress of spring, a common feature for arctic-breeding birds with a narrow time window in which to complete reproduction (Prop *et al.* 2003, Warnock *et al.* 2004).

Successful reproduction strongly depends on female body condition before breeding (Ebbinge & Spaans 1995, Alisauskas 2002, Drent *et al.* 2003) and female geese usually have higher AP scores than males during

pre-breeding (Boyd & Fox 1995, this study). Females from both breeding colonies gained similar amounts of fat reserves during their stay in Vårsolbukta, but males from Kongsfjorden gained more reserves compared to males from Nordenskiöldkysten. Hence, they build an energy buffer in order to cope with the less predictable conditions, in terms of food resources, at the subsequent site(s). Accordingly, Vårsolbukta is used as a stepping stone during migration with the possibility to rest and to supplement body reserves before the next step towards the breeding area (Kongsfjorden birds).

Stopover sites in Svalbard

Earlier studies have found considerable time gaps between departure from the Norwegian staging areas and arrival in the breeding areas of Svalbard for Barnacle Geese (Tombre *et al.* 1996, Prop *et al.* 2003). Vårsolbukta was suggested as a possible candidate stopover site where geese spend this time. However, Vårsolbukta cannot account for the entire time gap, since the travel time between Norway and Vårsolbukta (c. 24 h, Owen & Gullestad 1984), as well as the time elapsed between departure from Vårsolbukta and nest initiation was longer than would be needed for a direct flight. This was further confirmed by migration schedules of individual geese that were observed at several sites during migration (Fig. 4). More evidence for additional

stopover sites in Svalbard includes the finding that the nest initiation date was correlated with the departure date in Vårsolbukta for the local birds, but not for those breeding at a distant colony. The results suggest that geese adopt a "hopping" strategy (Piersma 1987, Skagen & Knopf 1994) using a chain of stopover sites whilst travelling through Svalbard during spring. This is also supported by studies utilising satellite transmitters (Glahder *et al.* 2006, Griffin 2008). Migrating in small steps between several sites may allow for better prediction of conditions at the next site. In this way, geese can adjust the timing of their migratory steps and their body reserves en route in response to external cues, as snow melt progresses and weather conditions ameliorate. When reaching the last stopover site in proximity to their breeding colony, geese wait until nest sites become snow free and can then time their move to the nesting location without losing the opportunity to replenish body reserves.

This study suggests that geese use stopover sites either as a buffer area for optimal feeding in proximity to the nesting site or as a link in a network of similar such sites. If such areas are disturbed or damaged, e.g. by natural reserves exploitation or tourism, the magnitude of the negative consequences will be different for different individuals and presumably also between years due to the stochasticity of the arctic environment. This applies not only to Barnacle Geese, but also Pink-footed and Light-bellied Brent Geese that usually use the same sites during spring (Mehlum 1998, Glahder *et al.* 2006, Hübner 2006). An increased knowledge of the network of stopover sites, including their function and utilisation by geese, will improve the possibility to protect such sites effectively.

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SAMENVATTING

Op het moment dat noordelijke ganzen gaan broeden is het broedgebied nog grotendeels bedekt met sneeuw. Voedsel vinden is dan een probleem, en de ganzen zijn daarom van lichaamsreserves afhankelijk om eieren te produceren. Daarnaast

moet het begin van het broeden afgestemd worden op het moment van dooi, wat niet gemakkelijk is omdat dat het ene jaar veel vroeger gebeurt dan het andere. Dit onderzoek ging in op de vraag hoe ganzen het klaarspelen om op het juiste moment en met voldoende lichaamsreserves op de plek van broeden aan te komen. Het onderzoek werd gedaan aan de op Spitsbergen broedende Brandgans *Branta leucopsis*, die in Scotland overwintert en tijdens de voorjaarstrek de kust van Noorwegen aandoet. Vogels die de meest noordelijke pleisterplaats in Noorwegen (Vesterålen) benutten, trokken eerder door naar Spitsbergen dan vogels die zuidelijker (in Helgeland) verbleven. Bovendien bleken de geringde vogels in Vesterålen hoofdzakelijk afkomstig van een kolonie in het noorden van Spitsbergen (Kongsfjorden), terwijl de ganzen in Helgeland ook zuidelijker broedden (Nordenskiöldkysten). Veel van de geringde ganzen werden direct na aankomst op Spitsbergen gezien op de berghellingen bij Vårsolbukta, waar de sneeuw door een gunstig klimaat eerder verdwijnt dan elders. Ganzen uit de noordelijke broedkolonie bleven maar 2,8 dagen op de berghellingen terwijl vogels die dichterbij nestelden gemiddeld 4,0 dagen pleisterden. Paren van de nabij gelegen kolonie verlieten de berghellingen regelmatig voor een korte tijd, waarschijnlijk om de situatie op de toekomstige broedplek te inspecteren. Tussen de dag van laatste waarneming op de berghellingen en het tijdstip van begin van de eileg bestond een positief verband. Althans dat gold voor de vogels van de nabij gelegen broedkolonie, maar niet voor vogels die noordelijker gingen broedden. De waarnemingen wijzen erop dat er een netwerk van pleisterplaatsen op Spitsbergen is waar de ganzen zich voorbereiden op het broeden. De plek die het dichtst bij de toekomstige broedplek ligt wordt als bufferplaats gebruikt, en de ganzen kunnen daarop terugvallen zolang de omstandigheden nog niet toelaten om te nestelen.   (JP)