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Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits

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On their way from the wintering area to the breeding grounds in Spitsbergen, barnacle geese *Branta leucopsis* stage on islands off the coast of Norway. The aim of this study was to describe when the geese migrate in relation to the body stores deposited and explore questions related to the concept of optimal migration schedules and on the possible mechanisms involved. We estimated fat stores by repeated assessments of the abdominal profile index of individually marked females throughout staging. Reproductive success was derived from observations of the same individuals later in the annual cycle. Females arriving late, or with low fat stores at arrival, achieved higher fat deposition rates, probably by spending more time foraging. But they were unable to match final fat scores of birds that arrived earlier or with larger fat stores. Reproductive success was correlated with the timing of migration and individuals departing at intermediate dates achieved highest success. The exact date of peak reproductive success depended on the size of fat stores accumulated, such that low-quality birds (depositing less fat) benefited most from an early departure to the breeding grounds. Observations in the breeding colonies showed that these birds did not initiate a nest earlier but they spent a longer time in Spitsbergen before settling. The length of stay in Norway was close to the prediction derived from an optimisation model relating spring events to eventual breeding success. Poorest performing birds stayed longer than expected, perhaps depositing more fat to avoid the risk of starvation. Two possible mechanisms of the timing of migration were contrasted and it seemed that the geese departed for migration as soon as they were unable to accumulate any more fat stores.

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Successful long-distance migration to avian breeding areas hinges on (i) the accumulation of sufficient body stores to cover costs of flight and (ii) appropriate departure and arrival times that optimise chances of reproduction (Alerstam and Lindström 1990, Madsen 2000). Because reproductive success is inversely related to date of egg laying in many migratory species (Daan et al. 1990), the decision when to migrate includes a trade-off between the benefits of an early arrival on the breeding grounds (= early migration) and the benefits of larger stores that can be obtained during a longer stay at migratory staging areas (= late migration). The fitness consequence of delaying departure for just a few days may be negated by late nest initiation. The optimal dates can be expected to differ among individuals depending on the precise shape of the various benefit curves (Alerstam and Lindström 1990, Møller 1994). To fully appreciate why and when birds migrate, information is needed on the dynamics of body stores of individual animals and the fitness consequences of the

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migration behaviour (Weber et al. 1998). Despite recent technological advancements in tracking large-scale movements in birds (Butler et al. 1998, Clausen and Bustnes 1998) the integration of behaviour and fitness is still a major hurdle in the understanding of migration patterns (Farmer and Wiens 1999). We studied this relatively unexplored field of migration ecology, combining work on the dynamics of body stores with the consequences that decisions during migration have for the fitness of the individual. We directed our attention to both the ultimate and proximate control (the mechanism) of the timing of migration.

The barnacle goose *Branta leucopsis* population that breeds in Spitsbergen is a good model species for migration studies because of the well-defined migration pathway (Owen and Gullestad 1984) and because many birds in this population are individually marked (Owen 1982). This allowed us to follow individuals throughout the pre-migratory season, assessing arrival and departure dates, and determining body condition and changes therein. Capitalizing on the long-term family bonds in geese, which may last over six months (Black and Owen 1989), we used brood size when pairs returned to the wintering area in autumn as a measure of fitness (Owen and Black 1989). Moreover, pairs observed during spring staging were traced to breeding colonies in Spitsbergen to investigate the relationship between the timing of migration and of breeding.

Two hypotheses concerning the mechanism of migration scheduling are depicted in Fig. 1. For both models we assume that individuals differ in quality, where high quality birds achieve highest deposition rates of body stores throughout staging, for example by being better competitors. This is depicted by different slopes of accumulated body stores prior to departure for the breeding grounds. The first hypothesis assumes that migration will take place as soon as a threshold in size of stores is reached. The threshold may be constant through time, or it may decline from an interaction with date (Drent and Daan 1980, Alisauskas and Ankney 1992). The second hypothesis assumes that migration will take place when the deposition rate of body stores can no longer be sustained. The latter mechanism applies for systems with a seasonal variation in food availability and we think this feature is typical for herbivores though not exclusive (Zwarts et al. 1990, Weber et al. 1998). Both models predict that high quality birds acquire largest stores, or stores are similar when the threshold of the 'size-of-stores'-hypothesis is constant (Fig. 1). The two models lead to different predictions regarding the timing of migration. The 'size-of-stores'-hypothesis predicts that high quality birds depart sooner than low quality birds. The 'deposition rate'-hypothesis predicts the reverse; high quality birds depart after low quality birds. We tested these predictions by checking the interrelationships between body condition at departure, individual deposition rates and date of departure. Realizing that body stores in migratory birds include different components we focused in this study on the accumulation of fat, which is the main substrate in terms of energy (Alerstam and Lindström 1990). In particular, we addressed the following questions. (1) Do fat deposition rates vary through the season? (2) Do body stores upon arrival vary through time, what are the average deposition rates, and how large are stores at departure? (3) Are individuals that arrive late in the season, or those with low body stores, able to compensate by depositing stores at a higher rate? (4) Do trends in individual deposition rates actually correspond to differences in foraging ability? We further determine the link between migration behaviour and fitness by separating the effects of timing of migration and the size of body stores on reproductive success. Finally, on the basis of fat deposition rates and time-related fitness measures, we modelled the expected optimal length of stay at migratory staging areas, and compared this with observations of individually marked birds.

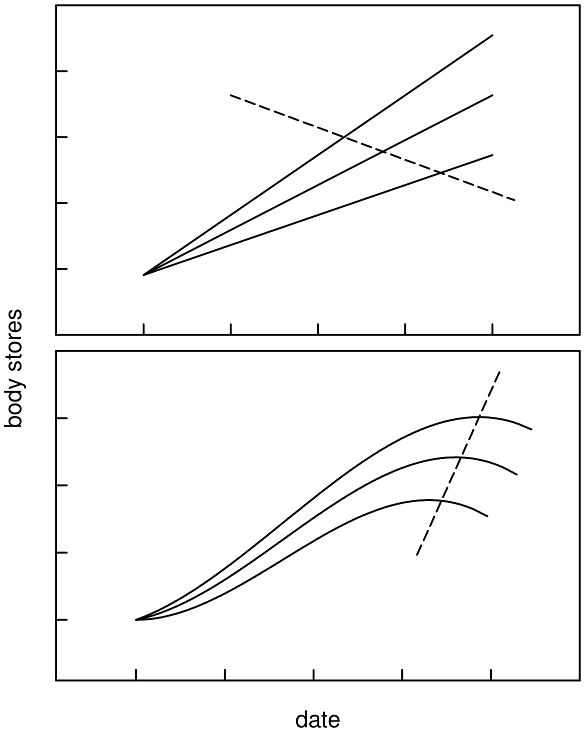

Fig. 1. Mechanism of the timing of migration in relation to body stores. The upper panel assumes a constant deposition rate through time, which varies among individuals (the three different curves). Birds depart for migration when reaching a threshold in the size of body stores (indicated by the dashed line). The departure threshold may be constant, or as is shown here it may decrease through the season. In this situation high quality birds acquire largest stores. In the lower panel environmental conditions deteriorate through the season, causing a decrease in deposition rates. Birds migrate when deposition rates begin to decline. In this situation high quality birds stay longer for example because they continue to monopolize feeding areas.

Methods

Study population

Data were collected in the coastal area of Helgeland, Norway (65°45′N, 12°E), in eight seasons (1980–1982 and 1989–1993). After wintering on the west coast of the UK, barnacle geese use the Norwegian stopover sites in April-May before the second leg of migration to the breeding grounds in Spitsbergen (Fig. 2). Study sites comprised the archipelagos of Laanan and Sandvaer, each consisting of a multitude of islands varying in size from few up to 15 hectares in area. The largest islands contained some houses which were inhabited by several families (Sandvaer) or which used to be permanently inhabited but were abandoned during the years of this study (Laanan). The archipelagos are isolated from other islands by open sea and thus each archipelago has its own local population of barnacle geese (Black et al. 1991). The vegetation types used by the geese ranged from poor quality hay meadows to salt marshes dominated by *Festuca rubra* and *Puccinellia maritima* (Prop et al. 1998). Additional observations were collected around the Solway Firth (Caerlaverock, Scotland) in autumn, as well as in Spitsbergen during summer.

Fig. 2. Map of the migration route of the barnacle goose breeding in Spitsbergen. Indicated are the wintering area (Solway), the spring staging area (Helgeland) and the breeding grounds (Spitsbergen).

Observations

Geese were individually recognizable by large leg rings with an inscription (Owen 1982) readable at a distance of up to 250 m. During the years of study, on average 20% of the whole Spitsbergen barnacle goose population was individually marked. The observers arrived in the area with the first geese or earlier (end of April or early May), and observations continued until most geese had departed (approximately 20 May). During the early morning hours, geese aggregated on the central islands where they were easily observed without disturbance. Most of the observations were collected during the first hours of the day (3–9 a.m.), although additional effort was made to identify geese later in the day as well when they foraged on more remote islands.

Abdominal profile

The abdominal profile (AP; Owen 1981) was used as an index for the extent of body fat deposits. Experienced observers can score the fatness of the birds in the field in an accurate and reliable way, without the need to recapture geese. AP's were assessed on a scale from 1 to 7. Dummy geese depicting different AP's were positioned on the main observation sites for consistent assessments within and among years. Studies in other goose species showed that AP classes (similar to ours) were linearly related to fat stores (Madsen et al. 1997, Boyd et al. 1998, Zillich and Black in press). We assume this holds for barnacle geese as well, and therefore treat the AP as an ordinal-scaled variable. Fat deposition rates through the season were analysed on the basis of AP's averaged by three-day periods per individual. Deposition rates were calculated as the increment in average AP from one three-day period to the next divided by the length of the interval. As a measure of individual fat deposition rate we calculated the quotient of the increment of the AP during the observation period and the number of days between first and last observation. In order to avoid autocorrelation when relating fat deposition rate to date of departure, data on fat deposition rates from the first half of the staging period only (up to and including 12 May) were used.

Reproductive performance

To interpret performance during spring migration in terms of fitness we counted the number of goslings associated with individually marked females in the following autumn, thus benefiting from the long duration of the parents-offspring bond (Black and Owen 1989). For further analyses pairs were classified as successful (with offspring) or failed (no offspring).

To relate the timing of reproduction to dates of migration, the date of settling, coinciding with laying the first egg, was recorded in breeding colonies in Spitsbergen (detailed in Prop and De Vries 1993). For this analysis a distinction was made between individuals that hatched at least one egg (successful breeders) and those that failed to hatch.

Ingestion rates

To test whether differences in fat deposition rates were related to foraging abilities we estimated individual ingestion rates. Ingestion rates can be calculated from the rate of fecal output (dropping mass × dropping rate) and food quality (Van Soest 1982). Given that food quality and dropping ates are largely date dependent (Prop and Black 1998), we simplified the calculation of ingestion rate by determining the residual dropping mass relative to date and time of the day (procedures of collection of droppings outlined in Prop and Black 1998). The residuals were averaged for each individual goose to obtain a single measure for relative ingestion rate. The average number of droppings collected per individual was 18.

Direct observations on migration

To assess the seasonal pattern of migration, observations of migrating birds were collected on an ad hoc basis. Migrating geese were clearly distinguishable from locally moving individuals by the type of vocalisations they made and by the structure of the flock. Birds arrived from the southwest and followed a narrow migration corridor along the outer islands (see also Bollingmo 1998), whereas birds that set off for migration headed north over the open ocean. Local flights were in any direction although easterly movements predominated.

Statistics and calculations

Some individuals visited the study islands only briefly, apparently on their way to other staging sites. For analyses we therefore selected birds that had been observed during the period of arrival (up to including 12 May) as well as during the period of departure (from 13 May onwards). As this study was concerned with those individuals that we assumed were most constrained in energetic terms during migration and reproduction we selected (i) females, which in geese invest more in the process of reproduction than males do (Ankney and MacInnes 1978), and (ii) birds that were older than three years of age because this is the first year of breeding in barnacle geese (Black and Owen 1995).

Dates of arrival and departure were taken from the first and last dates of observation. We cannot exclude that birds were missed occasionally and arrived earlier or departed later than actually observed, but the error is probably small. In all calculations dates were expressed as the number of days from 1 April. A standard statistical package (SPSS) was used for analyses. To test for significance of effects, linear or logistic regressions were performed following a procedure with backward elimination of variables. As a default for the probability associated with the F-test for exclusion of a variable we used SPSS 0.1 (1999). Year was included as a dummy variable in all analyses.

Results

Fat deposition rates through the season

Fat deposition rates varied through the season in a quadratic way (Fig. 3). After initially increasing the daily change in AP peaked at 0.15 units, followed by a rapid drop in the second half of the staging period (Table 1). Seasonal patterns in deposition rates did not differ among years.

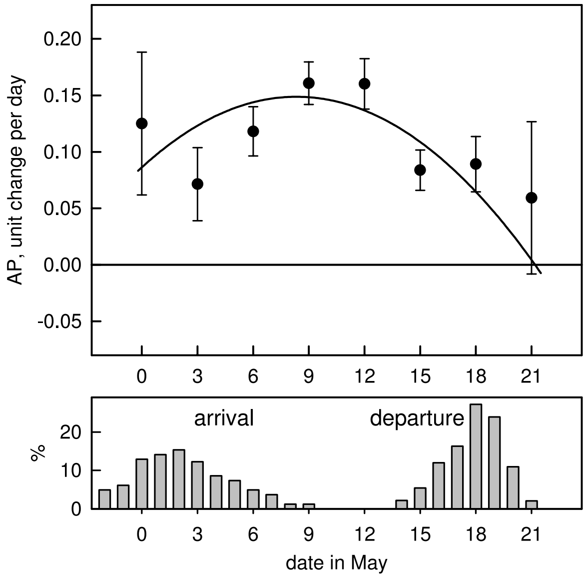

Fig. 3. Upper panel: variation of fat deposition rates through the season. The regression line is derived from the model in Table 1 for averaged arrival parameters. Data points (± SE) were adjusted for arrival parameters (total $n = 706$). The lower panel gives the relative distribution of birds observed arriving in ($n = 1520$) or departing from ($n = 3330$) the study area.

Table 1. Linear regression of fat deposition rate (daily change of AP) by date and year. Non-significant terms (N.S.) not included in the model shown within brackets.

term	coefficient	t	significance
constant	−1.67		
Date	0.0904	2.95	<0.005
Date	−0.0011	−2.93	<0.005
(Year)		1.31	N.S.

$F_{2,703} = 4.36$, $p < 0.05$.

Fat scores and timing of migration

Fat scores upon arrival and at departure were closely correlated (Table 2). We can draw two conclusions from the observed relationship (Fig. 4). Firstly, the slope of the regression was less than 1 (95% confidence interval 0.56–0.72), which indicates that the amount of fat deposited during staging (reflected by the increment between arrival and departure) was inversely related to AP at arrival. In other words, individuals that arrived with lowest fat stores deposited most during staging in the area. Secondly, because there was a positive relationship between AP upon arrival and at departure we conclude that birds arriving with low fat stores were unable to match the performance of birds arriving with large stores.

Birds arrived at the staging area with progressively larger fat scores during the season (Fig. 4; $y = 0.47 + 0.035x$, $F_{1,291} = 28.7$, $p < 0.0005$; or 0.035 AP units per day versus on average 0.10 units for individuals staging in the area). However, by the time they departed for the breeding grounds, AP scores of early arriving birds were larger than late arriving birds (Fig. 4). Apparently, the latter group had little time to accumulate the same amount of stores obtained by birds arriving earlier at the staging grounds.

AP at departure showed a quadratic response through time; after an initial increase the AP scores declined for birds departing after 17 May ($F_{2,363} = 42.45$, $p < 0.0001$; Fig. 5). The quadratic effect resulted from birds that arrived late or with few stores to depart late, because when adjusting for the effects of arrival parameters, AP at departure showed a linear relationship with date (Table 2). The birds seen departing at the end of the staging period obviously deviated from the general trend by having exceptionally low AP scores.

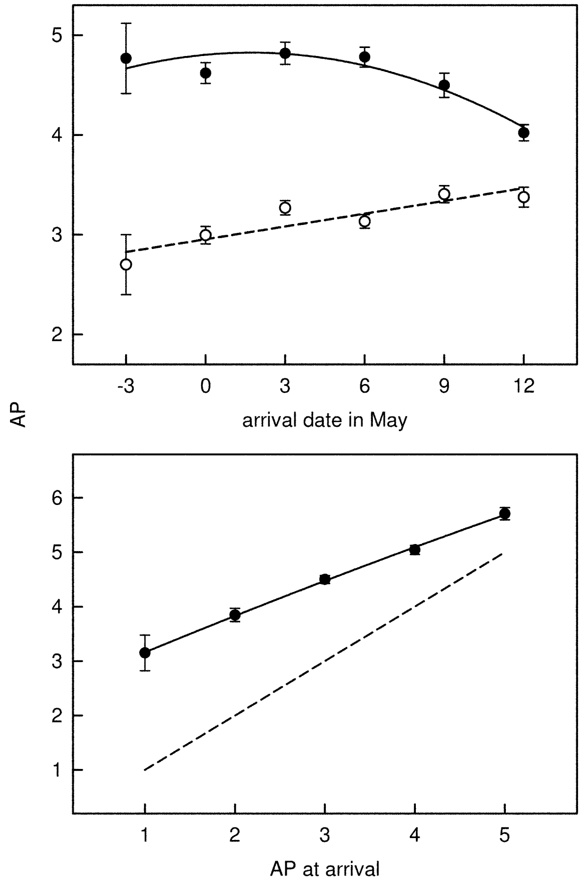

Fig. 4. AP at arrival (open symbols) and AP at departure (solid) in relation to arrival date (upper panel), and AP at departure in relation to AP at arrival (lower panel). Regression lines are derived from the model in Table 2 for an averaged date of departure, and averaged AP upon arrival (upper panel) or date of arrival (lower panel; total $n = 365$). The difference between the solid and dashed lines gives the amount of fat deposited during staging. Values are means ± SE.

Table 2. Linear regression of AP at departure by date of arrival, AP at arrival, and date of departure. Non-significant terms (N.S.) not included in the model shown within brackets.

term	coefficient	t	significance
constant	−14.66		
Date of arrival	0.679	3.64	<0.0005
Date of arrival	−0.010	−4.01	<0.0001
AP at arrival	0.643	15.23	<0.0001
Date of departure	0.136	6.07	<0.0001
(Date of departure)		−1.10	N.S.

$F_{4,360} = 91.51$, $p < 0.0005$.

Individual fat deposition rates and timing of migration

Individual fat deposition rates assessed during the first half of the staging period varied with date of arrival (positive effect) and AP at arrival (negative effect, Table 3). While adjusting for these effects, there was a positive relationship between deposition rate and date of departure (Fig. 5). Without adjustments the relationship showed a similar trend ($F_{1,190} = 14.11$, $p < 0.0005$).

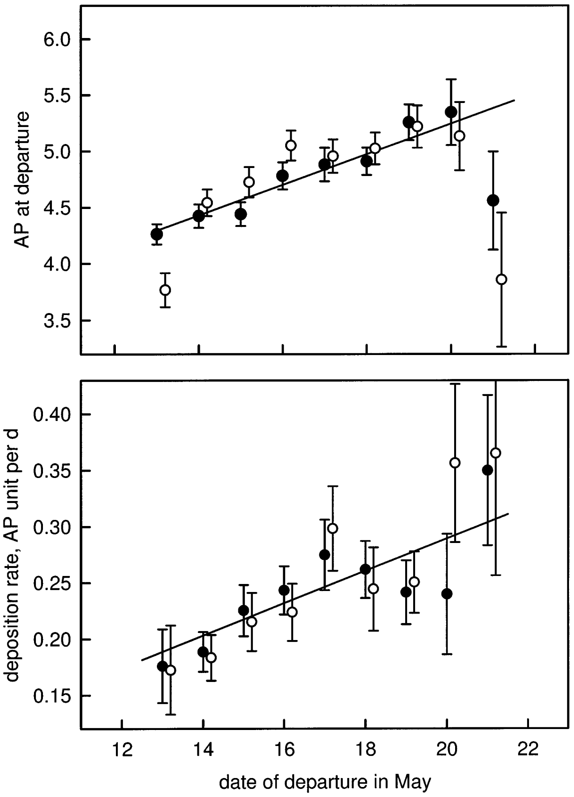

Fig. 5. The relationship between AP at departure and the date of departure (upper), and deposition rates during the first half of the staging period averaged by individual in relation to the date of departure (lower). The regression lines are derived from the models in Table 2 (total $n = 365$) and Table 3 (total $n = 192$) for averaged arrival parameters. Filled symbols represent observations (± SE) adjusted for arrival parameters; open symbols are unadjusted values.

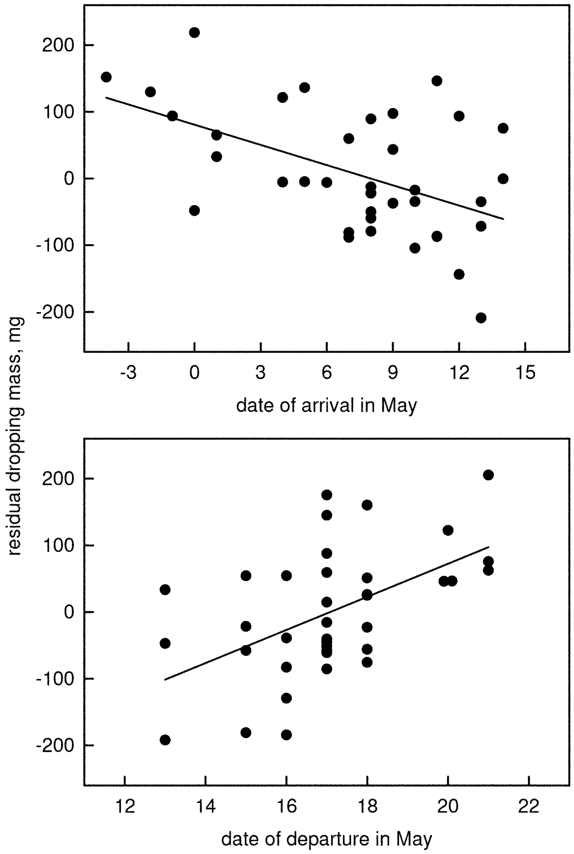

Fig. 6. Relationship between residual dropping mass and date of arrival (upper), and date of departure (lower). Regression lines are derived from the model in Table 4 ($n = 37$). Observations in the two plots were adjusted for each other.

Food ingestion rates and timing of migration

Residual dropping mass, as an indicator for individual food ingestion rate, was positively related to date of departure (Fig. 6). Thus, trends in fat deposition rate and relative ingestion rate in relation to date of departure ran parallel, which suggests a causal relationship; i.e. late departing individuals achieved larger body stores because they were better foragers. In contrast, residual dropping mass was negatively related to date of arrival, and unrelated to AP at arrival (Table 4). Thus, individuals that arrived late or with few stores performed relatively poorly in terms of food ingestion rates. This means that the higher fat deposition rates observed in these individuals cannot be attributed to higher instantaneous rates of food intake.

Table 3. Linear regression of fat deposition rate (daily change of AP) by date of arrival, AP at arrival, and date of departure. Non-significant terms (N.S.) not included in the model shown within brackets.

term	coefficient	*t*	significance
constant	−0.96		
Date of arrival	0.0225	7.88	<0.0005
AP at arrival	−0.079	−7.63	<0.0005
Date of departure	0.0144	3.11	<0.002
(Date of departure)		−1.16	N.S.

$F_{3,\ 188} = 39.88$, $p < 0.0005$.

Table 4. Linear regression of residual dropping mass (as a measure of food intake rate) by date of arrival, AP at arrival, date of departure, and year.

term	coefficient	*t*	significance
constant	−37.26		
Date of arrival	−10.21	−3.59	0.001
(AP at arrival)		0.71	N.S.
Date of departure	24.83	3.61	0.001
(Year)		1.69	N.S.

$F_{2,\ 34} = 13.18$, $p < 0.0005$.

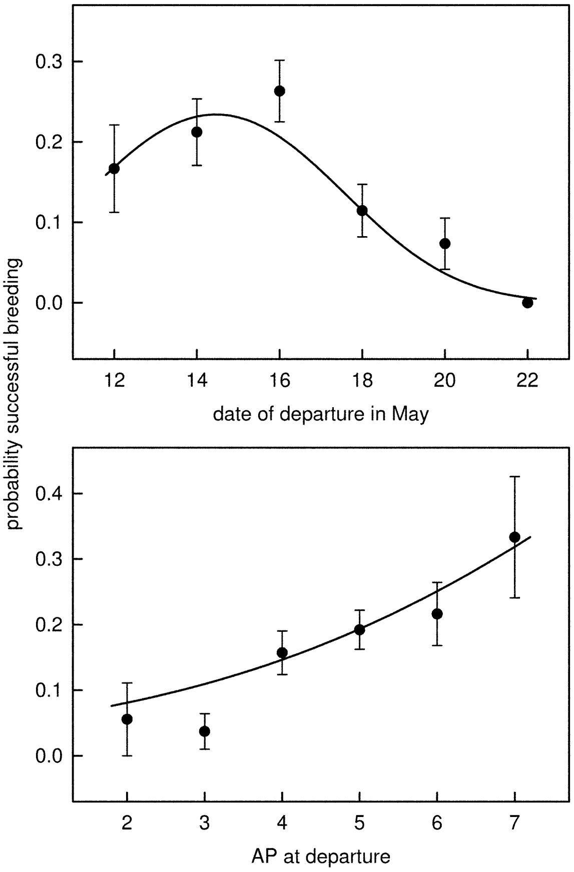

Fig. 7. Reproductive success in relation to the date of departure (upper), and in relation to AP at departure (lower). Regression lines were derived from the model in Table 5, averaged across years and for average AP at departure (upper) or for average date of departure (lower). Values are means ± SE (total $n = 454$).

Reproductive success and timing of migration

Reproductive success showed a quadratic relationship with date of departure; individuals departing at intermediate dates achieved highest success whereas early and late birds performed less well (Fig. 7). Given the interaction term between AP and date of departure (Table 5), the variation of reproductive success by date depended on the final fat score. With increasing AP at departure the peak reproductive success shifted towards later dates. Irrespective of the date of departure, reproductive success was positively related to AP. Typical for arctic-breeding birds (Remmert 1980) reproductive success showed a large amount of variation among years (Table 5).

Table 5. Logistic regression of reproductive success in relation to date of departure (date), AP at departure (AP), and year ($n = 454$). Non-significant terms (N.S.) not included in the model shown within brackets.

term	coefficient	deviance	df	significance
Date	6.56	5.43	1	<0.05
Date	−0.081	6.17	1	<0.025
Year		64.62	7	<0.0005
Date × AP	−0.11	3.26	1	0.071
Date × AP	0.003	3.71	1	0.054
Constant	−137.1		1	
(AP)		0.30	1	N.S.

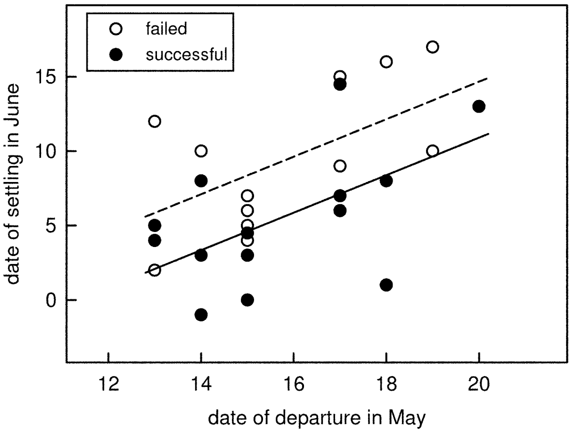

Fig. 8. Relationship between date of settling in Spitsbergen and date of departure from Norway for failed and successful breeders separately. The averaged regression line is $y = 10.74 + 1.26x$, $n = 26$.

Date of departure from the staging area and timing of breeding in Spitsbergen were positively related (Fig. 8; $F_{1,23} = 11.1$, $p = 0.003$). This means that the nest initiation dates in Spitsbergen were strongly linked to the timing of migration from the southerly staging area. The gap between departure and settling in the breeding colony was 3 weeks. Relative to the date of departure, failed breeders started breeding 4 days later than successful birds ($F_{1,23} = 5.89$, $p < 0.025$).

Optimal length of stay

Above we established the interrelationships between fat deposition rates and arrival parameters (AP and date) on the one hand, and reproductive success and departure parameters on the other. Based on these relationships we modelled the optimal length of stay depending on when the birds arrived and with how much fat. Seasonal patterns in fat deposition rates (Table 1) enabled us to calculate the amount of stores accumulated. Fig. 9 (upper panel) gives an example for birds arriving on 5 May, with AP's varying from 1 to 5. Subsequently, for each date the probability of successful breeding (following Table 5) was calculated (Fig. 9, lower panel). Thus, for any combination of arrival date and AP at arrival the departure date that gives maximal reproductive success can be determined. Similarly, we calculated how long individuals should stay in the area to maximize reproductive success. These optimal

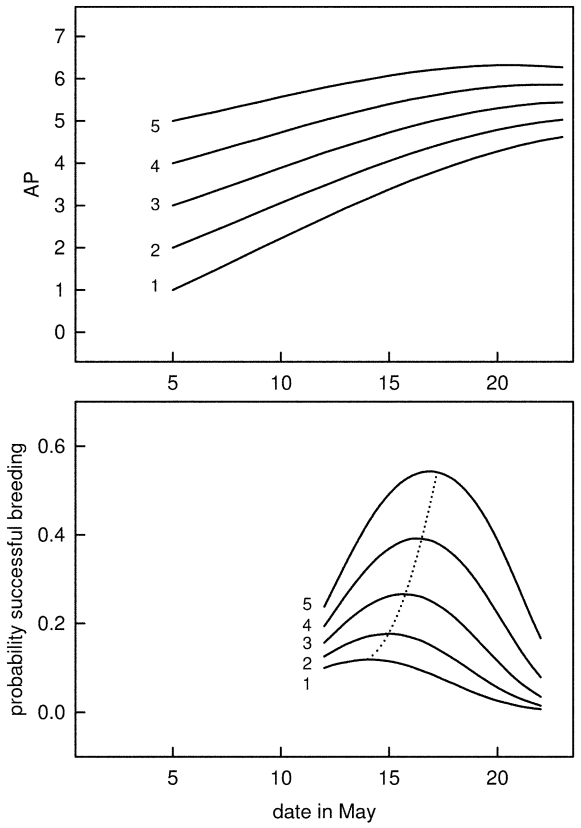

Fig. 9. Upper panel. Example trend in AP for individuals that arrive on a particular date (5 May) and with different AP's (based on a model of fat deposition rates that includes date, Table 1, and arrival parameters, Table 3). Lower panel. Probability of successful reproduction derived from date and associated AP in the upper panel and based on the model in Table 5. The AP at arrival associated with each of the curves is indicated at the left.

lengths of stay have been plotted against the date of arrival and AP at arrival (Fig. 10). Optimal length of stay was inversely related to the date of arrival, such that any delay in arrival caused a similar reduction in the optimal length of stay. In contrast, the optimal length of stay was positively related to the amount of fat stored. On average there was a three-day difference between the extreme AP scores in Fig. 10.

Results are summarized in Fig. 11, which shows the decline in optimal length of stay with later arrival dates. The actual observed lengths appear to match the optimal values well (Fig. 11) although birds arriving later tended to stay longer than expected. In relation to the AP at arrival there is a close match between optimal and observed values as well, except for birds that arrived with the thinnest fat scores who remained on the staging area for longer than expected. We conclude that for most individuals the time spent in the area corresponded to the optimal lengths of stay.

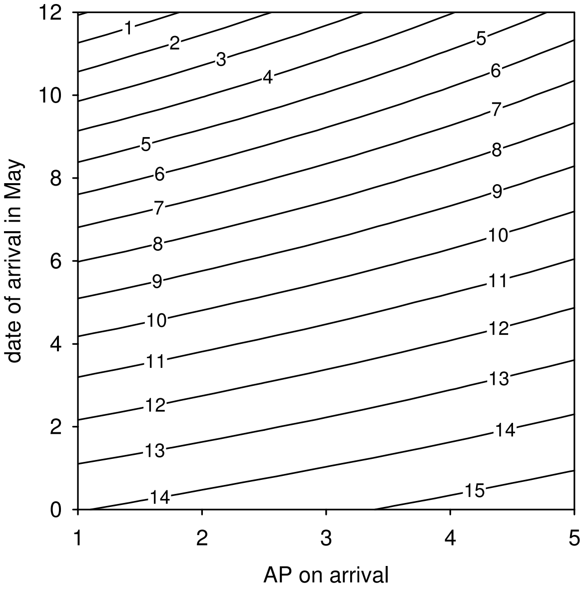

Fig. 10. Isolines for the optimal length of stay (in days) for combinations of date of arrival (y-axis) and AP at arrival (x-axis).

Discussion

This study showed a close correlation between premigration performance and reproductive success. First, reproductive success was correlated with the date of departure from the staging area, with highest success for birds departing at intermediate dates. Reproductive success as a function of its timing has been established in a plethora of studies (Perrins 1970). However, only few studies showed that the basis for a proper timing of reproduction is already founded before arriving on the breeding grounds (Sandberg and Moore 1996, Marra et al. 1998). Below we discuss the interrelationships between date-dependent reproductive success and the decision on when to migrate. Secondly, the probability of successful breeding was correlated with the amount of fat accumulated. This agrees with the supposed importance of internal stores for geese to produce a clutch and to hatch the eggs successfully (Drent and Daan 1980, Ebbinge and Spaans 1995). Our observations do not necessarily imply that reproduction is totally dependent on body stores, this is unlikely given that barnacle geese feed a lot on the breeding grounds (see below), but the observations do support the idea that large stores provide a head start for successful reproduction.

Do the fittest individuals migrate first?

The trade-off that spring staging birds face is either to stay longer to accumulate more body stores, or to depart to benefit from early arrival on the breeding grounds. Benefits associated with early arrival can in-

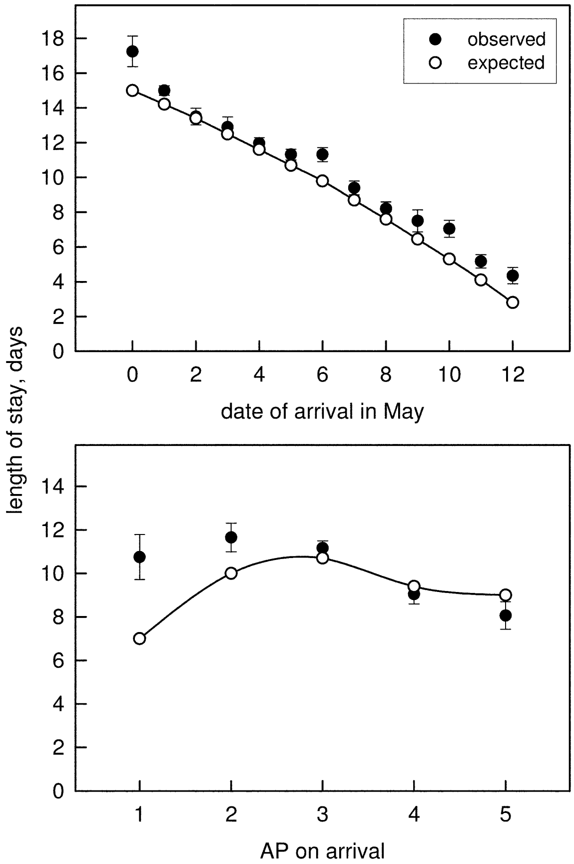

Fig. 11. Length of stay in relation to date of arrival (upper) and AP at arrival (lower) (total $n = 293$). Observed averages ($\pm$SE) are compared with the expectations based on the model in Fig. 10.

clude reducing competition for food, or better opportunities to occupy the best nesting sites (Kokko 1999). Clearly, arrival in the breeding area is constrained by extensive snow cover, which impairs finding food early in spring and which may result in impaired nest success for early settlers (Prop and De Vries 1993). On the other hand, costs of early arrival in barnacle geese are offset by a better survival rate for early-hatched goslings (Prop and De Vries 1993). Which time of migration suits an individual best (the optimal time) depends on the quality of the individual (Møller 1994), and usually it is thought that there is a gradient with highest quality birds being first to migrate (Drent and Daan 1980, Francis and Cooke 1986, Marra et al. 1998). Our results on barnacle geese indicate otherwise: the first birds to leave the staging areas were the poorest ones achieving lowest ingestion rates and departing with smallest fat stores. This agrees well with observations in Spitsbergen on the same goose population by Tombre et al. (1996) showing that later arriving birds had larger body stores. In this manner geese behaved optimally, as suggested by our models on the timing of migration. First, the optimal date of departure was earlier for individuals that performed poorly (Fig. 9). Individuals that were unable to accumulate large stores had the best chance for successful reproduction by departing early to the breeding grounds. Secondly, the observed lengths of stay were close to the predicted optimal values (Fig. 11). Exceptions were individuals that arrived with few stores or that arrived late in the season because these birds stayed longer than expected. The reason for this discrepancy might be that predictions were based on short-term reproductive success which did not account for effects of the size of fat stores on survival probabilities. The amount of energy required for migration and maintenance costs during the early stay on the breeding grounds are substantial and data on pink-footed geese *Anser brachyrhynchus* suggest that a considerable amount of fat is required to survive through spring snow-melt (Drent et al. 2003). We suggest that in order to avoid the risk of an early death barnacle geese employ a lower threshold of body stores which enables them to survive the period of low food abundance.

Does early migration mean early breeding?

Because dates of migration and settling in the breeding colony were correlated (Fig. 8), we expect that the relationship between reproductive success and date of departure reflected the seasonal pattern in reproductive success relative to the date of settling. In general terms this was the case, with a progressive decline in success with advancing settling dates (Prop and De Vries 1993). There were however striking differences in the two seasonal patterns. First, the range of dates of settling (18 days) was considerably larger than the range of migration dates (7 days). Secondly, the depressed success visible in early migrants was much less pronounced, if present at all, in early settlers. Apparently, during the chain of events between departure for migration and settling in the breeding colony the order of goose pairs was re-arranged: early migrants settling relatively late, and birds that migrated late settling early. Indeed, there was a large variation among individuals in interval between migration and settling in the colony (in similarity to the variation in time between migration and arrival in the vicinity of the breeding colony, Tombre et al. 1996), and notably intervals were largest for birds that eventually failed to hatch the eggs (Fig. 8). Given that the distance to Spitsbergen can be covered within 24 flight hours (Owen and Gullestad 1984, Butler et al. 1998), coupled with the finding that the time required to occupy a territory is 2–3 days (Prop and De Vries 1993), most of the time between migration and settling is spent on snow-free patches where extensive feeding is possible as long as environmental conditions allow (Prop and De Vries 1993), which is similar to patterns observed in other goose species (Fox and Madsen 1981, Bromley and Jarvis 1993, Ganter and Cooke 1996). The earliest barnacle geese settle on 30 May (Løvenskiold 1964), which indicates a pre-laying time in Spitsbergen of 12 days (assuming departure from Norway on 17 May). This is identical to the time required for development of eggs (12–13 days, Alisauskas and Ankney 1992). For most individuals the interval is longer (Fig. 8) which supports the idea that foraging conditions, and perhaps availability of nest sites, limit the onset of breeding (Ganter and Cooke 1996).

Our observations provide an interpretation of the benefit of early migration that differs from previous suggestions. Rather than breeding early, the advantage that accrues to migrating early for poor-quality birds is that they have extra feeding time available to prepare for egg-laying. In this manner they avoid initiating a nest at a late date, in addition to the benefit of avoiding competition when arriving early (Nolet and Drent 1998).

The mechanism of the timing of migration

We found strong support for the 'deposition rate' hypothesis, which suggests that geese decide to migrate when fat deposition rates drop to a lower threshold. Firstly, because the pre-condition of a seasonal change in deposition rates were met. Secondly, because two predictions of the 'deposition rate' hypothesis were upheld. The AP at departure increased through time; and the same appeared to be the case for the individual deposition rate.

The seasonal variation in fat deposition rates may have had various causes. Geese accumulate protein during pre-migration in addition to fat (Alisauskas and Ankney 1992). Deposits are mainly located in the breast muscles and are thus not accounted for in the AP score. A decrease in fat deposition might reflect a shift to the accumulation of protein. This explanation is unlikely as the seasonal pattern of protein deposition, with highest rates mid-season, is similar to that of fat (Prop and Black 1998). Also, fat deposition rates could be a reflection of the efforts of the geese to collect food. For example waders show a decrease in fat gain immediately before departure by spending less time feeding (Zwarts et al. 1990). Occasionally we observed a similar behaviour in barnacle geese by birds resting for 12-24 hours prior to take-off but this time span was too short to affect trends in deposition rate reported in this paper. Instead, as a most likely explanation for the seasonal trend in deposition rates we regard the effects of food resource availability. Being strict herbivores, geese are sensitive to changes in the availability and the quality of the food (Krapu and Reinecke 1992). An increase of food availability caused an increase in fat deposition rate early in the season and a decline in food quality through time produced the subsequent decline (Prop and Black 1998). Also the pattern in deposition rates observed in this study fit well with productive energy available for fat store deposition in the same population (Prop and Black 1998).

An important implication of the 'deposition rate' hypothesis is that deteriorating foraging conditions trigger migration. Birds migrate at a point when it is no longer profitable to remain in a particular area. In fact this is the basic idea of the green-wave hypothesis (Drent et al. 1979), which implies a similar mechanism. It also explains why a substantial proportion of spring staging geese, as observed in several species, take off for migration before they have deposited any substantial amount of fat (Boyd et al. 1998, Boyd 2000).

The lower threshold of fat accumulation is a likely strategy for animals that live in environments that are characterized by seasonal fluctuations in food availability, as for (migratory) herbivores in general (Albon and Langvatn 1992). Animals that use agricultural habitats may employ a different strategy because of the generally larger food abundance and higher food quality. Rather than a threshold in deposition rate, in these richer systems the alternative 'mass-threshold' may hold. Indeed, individuals of the same barnacle goose population that staged on agricultural fields obtained more fat and stores were deposited at a higher rate (Prop and Black 1998).

Fat deposition rates: individual variation in deposition rates

In arctic-breeding geese large energy stores deposited during spring staging are thought to be a prerequisite for successful migration and reproduction (Madsen 2000). Individuals achieving high fat deposition rates are therefore positively selected for. Variation in deposition rate among individuals can be expected to depend on differences in foraging abilities. Indeed, this is supported by the close correspondence in seasonal trends in fat deposition rate and in food ingestion rate (Fig. 6 and 7). The observations thus imply a direct link between foraging behaviour and the size of fat stores deposited. However, the higher deposition rates in individuals that arrived late or with few stores were not correlated with higher food ingestion rates. Instead, late arrival appeared to correlate with lower food ingestion rates (Fig. 6). Birds that (partially) compensated for late arrival or low body stores at arrival must have obtained the additional body stores somehow and we suspect they did so by spending more hours foraging per day. This may have included earlier arrival on the feeding grounds in the morning, later departure to the roost, and shorter resting spells throughout the day. If true, this would be a parallel to the performance between different populations in bar-tailed godwits *Limosa lapponica* during pre-migratory fattening (Scheiffarth et al. 2002). Those populations differed in the amount of time spent foraging per day which explained the differences in rate of deposition of body stores. We expect that there are fitness costs associated with more intensive foraging because increasing foraging time entails an increased risk of being predated (Metcalfe and Furness 1984, Whitfield et al. 1988). Although we rarely observed geese being predated, potential predators were abundant in the area (white-tailed eagle *Haliaeetus albicilla*, eagle owl *Bubo bubo*, mink *Mustela vison*). Similarly, Madsen (1998) suggested a trade-off between food intake and predation risk in pink-footed geese.

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