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Intake rates, stochasticity, or onset of spring – what aspects of food availability affect spring migration patterns in Pink-footed Geese *Anser brachyrhynchus*?

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Long-distance bird migration consists of several flight episodes interrupted by a series of resting and refuelling periods on stopover sites. We assessed the role of food availability as the determinant of staging decisions focusing on the following three aspects of food availability: intake rate, stochasticity in intake rates and onset of spring. Using stochastic dynamic modelling, we investigated their impact on staging times and expected fitness. Subsequently, we compared relations in the use of the stopover sites as predicted by the model with empirical data of the Svalbard-breeding population of Pink-footed Goose *Anser brachyrhynchus* collected in the period 1990–2002.

Our results indicate that, for the case of Pink-footed Geese, spring phenology determines a major part of the migration schedule. In contrast to our expectations, intake rates were generally only of minor importance; however, when approaching the breeding grounds their significance increased. Expected fitness at arrival on the breeding grounds showed that the geese can compensate for changes in a broad range of food availability and also cope with varying degrees of stochasticity. However, declining intake rates at the last stopover site or very late onsets of spring clearly decreased fitness.

As predicted by the model, the use of stopover sites was interdependent – from empirical data we derived negative relationships between the staging durations of subsequent sites. These results lend credit to an integrated spatially explicit approach focusing on multiple stopover site characteristics when attempting to improve our understanding of bird migration.

Key words: stochastic dynamic model, *Anser brachyrhynchus*, stopover duration, interdependent stopover site use, arctic breeder

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INTRODUCTION

For long-distance migrants, the migration between wintering and breeding grounds has been identified a major event in the birds’ annual cycle, often impinging heavily on their reproductive success. To maximise reproductive output, migratory birds are assumed to optimise the journey as the timing and energetic state at arrival are likely correlates of their fitness (Alerstam & Lindström 1990, Clark & Butler 1999, Kokko 1999, Prop et al. 2003, Bauchinger & Klaassen 2005). In contrast to extensive theoretical studies on the optimization of migratory flights (e.g. Butler et al. 1997, Hedenström 1993, Klaassen et al. 2000, Battley et al. 2001), surprisingly little effort has been invested into theoretical investigations on stopover site use. However, some studies have already highlighted specific aspects of conditions on stopover sites, e.g. predation pressure (Weber et al. 1998, Ydenberg et al. 2002), human disturbance (Klaassen et al. 2006), and food availability – in particular, intake rates (Alerstam & Lindström 1990, Klaassen & Lindstrom 1996) – have been shown to influence staging decisions on stopover sites.

Average migration speed is usually not limited by flight speed but rather by the rate of fuel accumulation (Hedenström & Alerstam 1998), the latter mainly depending on conditions on stopover sites. Therefore, the choice of staging sites, decisions on how long to stay and how intensively to feed are key mechanisms, which affect a bird’s fate during migration and ultimately its fitness (Alerstam & Lindström 1990, Dierschke & Delingat 2001, Erni et al. 2002).

As the purpose of stopover sites is to allow refuelling between migratory steps, they should provide sufficient food in a particular time window. Food availability can be characterised by three aspects, which may vary independently – (1) intake rate, as an integrated measure of food quantity and quality, (2) stochasticity in intake rates and (3) onset of spring, which determines the date from which food is available on a given site.

To investigate the impact of each of these aspects on staging times at migratory stopover sites we developed a stochastic-dynamic model for avian spring migration, with which we calculated the optimal itineraries and predicted migration schedules. Varying the abovementioned aspects of food availability allowed us both to estimate the role each of these factors plays in determining staging times and to identify environmental variables birds potentially use in departure and staging decisions. To scrutinize our model predictions, we compared model findings with empirical migration schedules of the Svalbard-breeding population of Pink-footed Geese Anser brachyrhynchus (Madsen 2001).

METHODS

Study population

The Svalbard-breeding population of Pink-footed Geese winters in Denmark, The Netherlands and Belgium. During March and April, the population gathers in Denmark, before migrating via Norwegian stopover sites to the breeding grounds. Traditionally, the geese have stopped in Vesterålen, northern Norway, but since the late 1980s, increasing numbers of geese have additionally used the Mid-Norwegian Trondheimsfjord area as stopover site (Fig. 1). Hereafter, the stopover sites Denmark, Trondheimsfjord and Vesterålen will be referred to as S1, S2, and S3, respectively.

During spring in S1, the geese show a great preference for newly sown cereal fields and to alleviate damage to these crops, geese are successfully baited with grain at five sites (Madsen 1996). In S2, the geese feed on fertilized pastures, stubble grain fields, and turn also gradually to newly sown cereal fields (Madsen et al. 1997). In S3, the geese primarily feed on fertilized pastures (Tombre et al. 2005). During the springs of 1990–2003, a total of 1810 Pink-footed Geese, of which 807 were females, were captured by cannon-netting, mainly in S1. All geese were aged and marked with a blue plastic neckband with a three digit individual code. As an evaluation of body condition, abdominal profile indexes (API) of marked individuals were visually scored by trained and inter-cal
brated observers (for standards and indexes, see Madsen et al. 1997). Resighting efforts were generally high in S1 and S3 throughout, whilst in S2 effort varied greatly between years, with a peak effort in 1996. Resighting data allowed the calculation of stopover staging times using the earliest and latest date at which a particular individual was seen on a site. As this procedure inherently underestimates staging times and to include sites and years with variable resighting efforts, we considered only those individuals in our analyses that were sighted on different stopover sites within a 5-day period, which yielded a sample size of 239 individuals. Comparing APIs at arrival and departure allowed us to estimate gain rates for each stopover site, which resulted in values of 1970, 2868, and 4038 kJ d⁻¹ for S1, S2, and S3, respectively (Fig. 1).

Figure 1. The spring migration flyway of Pink-footed Goose Anser brachyrhynchus stretches from Jutland, Denmark (S1) via two major stopover sites in mid and North Norway (S2 and S3), a pre-breeding site in Svalbard to the breeding grounds in Svalbard (right panel). For each stopover site, the intake rates were estimated from abdominal profile recordings after arrival and before departure (right panel, solid lines). Food availability functions may differ in three aspects as schematically indicated (grey lines) – intake rates (solid grey line, exemplarily shown for S1), stochasticity in intake rates (dotted and dashed grey lines, exemplarily shown for S2) and onset of spring (solid grey line, exemplarily shown for S3).
The dynamic model

We used dynamic programming to find the sequence of migratory decisions that would maximise the fitness of the female Pink-footed Goose under various environmental conditions encountered during spring migration. The dynamic program largely followed the concepts presented by Weber et al. (1998, 1999) and Beekman et al. (2002). We distinguished five potential staging sites \( i \): the three main stopover sites (Denmark S1, Trondheimsfjord in central Norway S2, Vesterålen in northern Norway S3), a pre-breeding site in the coastal areas of Svalbard and the breeding site (Svalbard). The distances \( D_i \) between these sites are 780, 630, 1130 and 10 km. The migration period was divided into whole days \( t \). Preparations for spring migration were assumed to start in S1 on 21 March (day 1).

We assumed that at time \( t \), the expected future fitness \( F \) of a female Pink-footed Goose, is a function of its body reserves \( x \), and its location \( i \): \( F(x,t,i) \). Body reserves may vary between 0, where the Pink-footed Goose used in our simulations reaches a body mass of 2.4 kg and dies of starvation, and \( x_{\text{max}} \), where the maximum reserve load of 32 082 kJ is reached at a body mass of 3.6 kg. At the breeding or destination site \( N \), the expected future fitness is \( F(x,t,N) \). For each time step when the goose has not yet arrived at its destination, it has two behavioural options: either foraging at intensity \( u \) (\( 0 \leq u \leq 1 \)) or, if fuel stores permit, flying to one of the next sites.

With the dynamic programming equations presented below, a matrix is compiled containing the optimal decisions for all combinations of body reserves, times and sites. This decision matrix allows us to follow the fate of individual birds during their migratory journey, i.e. the timing and intensity of use of the various sites along the migration route. As many of the dynamic programming equations follow earlier studies (Weber et al. 1998, Weber et al. 1999, Beekman et al. 2002), we provide only a brief description here emphasizing the differences with the earlier models.

Expected fitness in terms of young produced at the destination \( (i = N) \) and in future years is a function of state upon arrival \( K(x) \), date of arrival \( K(t) \) and expected fitness from future breeding attempts \( B(x) \):

\[
F(x,t,N) = K(t) \cdot K(x) + B(x)
\]  
(1)

Empirical data suggest that successful breeding is only possible if geese arrive at the breeding grounds in a rather narrow time window. Therefore, the optimal period of arrival at the breeding grounds was set between 20 and 26 May (Julian day 140–146).

\[
K(t) = \begin{cases} 
0 & \text{if } t \leq 140 \text{ or } t > 146 \\
1 & \text{if } 140 \leq t \leq 146 
\end{cases}
\]  
(2)

The state at which the Pink-footed Goose female arrives on the breeding grounds also importantly determines its breeding success (Madsen & Klaassen 2006, Madsen & Klaassen unpubl.):

\[
K(x) = \frac{1}{2} \left( \frac{e^{w(x-xc)} - e^{-w(x-xc)}}{e^{w(x-xc)} + e^{-w(x-xc)}} + 1 \right)
\]  
(3)

where \( w \) and \( xc \) were set to 0.028 and 73, respectively.

If the female and its mate are unable to complete their migratory journey successfully the females’ expected fitness equals \( B(x) \). According to J. Madsen & M. Klaassen (unpubl.) the survival, and therewith the expected future reproductive fitness of Pink-footed Geese, is positively related to the state of the geese upon arrival at the breeding grounds. We thus approximated the lifetime future reproductive success of the geese as:

\[
B(x) = B_T \cdot (a_0 + a_1 x + a_2 x^2)
\]  
(4)

where \( B_T \) was set to 2, to resemble the approximate average life-time reproductive success of females in a stable population and \( a_0, a_1, \) and \( a_2 \) were set to 0.773, 8.3 \times 10^{-4} \) and 3.6 \times 10^{-6} respectively, to mimic the effect of state upon arrival on survival (J. Madsen & M. Klaassen unpubl.).

The maximum intake rate that a foraging goose may attain is site and time dependent \((g(i,t), \text{kJ d}^{-1})\). The actual intake rate is determined by the foraging intensity \( u \). How much of this intake rate ultimately is stored as body stores
depends on the energy expenditure \( e \) (kJ d\(^{-1}\)). Maintaining fuel stores incurs a fitness cost in terms of increased risks of predation and injury (Witter & Cuthill, 1993):

\[
\beta(x,u) = m_\beta \frac{(x + ug(i,t) - e)^{a+1} - x^{a+1}}{(a + 1)(ug(i,t) - e)}
\]

(5)

where \( m_\beta \) was set to \( 10^{-8} \) and \( a \) was set to 2 (Madsen \textit{et al.}, 2002).

If the Pink-footed Goose decides to forage, it should forage with an intensity \( u \) that yields the maximum expected fitness at the destination:

\[
H_f(x,t,i) = \max_u [(1 - \beta(x,u))F(x + ug(i,t) - e, t + 1, i)]
\]

(6)

Alternatively, an individual can depart to the next site depending on its fuel stores \( x \) and the distance \( D \) (km) to the destination site. Its fuel stores upon arrival at the destination \( x_a \) were calculated using

\[
x_a = \frac{c^2}{(c - (c(1 - (1 + x/x_{max})^{-0.5} - D))^2} - 1 \cdot x_{max}
\]

(7)

where \( c \) is a flight range parameter which is calculated using

\[
c = \frac{D_{\max}}{1 - (1 + x_f / x_{\max})^{-0.5}}
\]

(8)

and \( D_{\max} \) is the maximum flight range when dedicating fraction \( x_f \) of the maximum fuel load \( x_{\max} \) to flight. For Pink-footed Geese in this study we used \( x_f = x_{\max} \). \( D_{\max} \) was calculated from the maximum fuel load and the flight costs:

\[
D_{\max} = \frac{x_{\max}}{v}
\]

(9)

If an individual decides to depart, it should fly to the site \( j \) yielding the maximum expected fitness at the destination:

\[
H_d(x,t,i) = \max_j [F(x_a,t + (\sum_{z=1}^{j-1} D_z / v), j)]
\]

(10)

where \( v \) is flight speed, which was estimated at 979 km d\(^{-1}\) following the allometric equation provided by Clausen \textit{et al.} (2003). The optimal decision is the behavioural alternative, foraging or departing, yielding the highest future expected reproductive success:

\[
F(x,t,i) = \max[H_f(x,t,i), H_d(x,t,i)]
\]

(11)

For computational reasons \( x, t, \) and \( i \) must be whole numbers. In the dynamic program we therefore adopted a whole number unit of energy which was equivalent to 321 kJ.

With the dynamic programming equations presented above, a matrix can be compiled containing the optimal behavioural decisions for all combinations of fuel stores, time and site. In subsequent forward simulations, geese are tracked in their spring migration while basing their decisions on the optimal decision matrix. Consequently, we can predict staging times and body reserve dynamics from these simulations and compare them with empirical data.

Model scenarios

In three corresponding scenarios, we systematically changed the model’s parameter settings for each of the three aspects of food availability: intake rate, stochasticity in intake rates, and onset of spring. In the ‘intake rate scenario’ we varied intake rates \( g_i(t) \) between 5 and 11 MJ d\(^{-1}\) in steps of 2 MJ d\(^{-1}\) covering the empirical range of daily increases in abdominal profiles (see Fig. 1). In the ‘stochasticity scenario’, day-to-day variability in intake rates was varied between no variability at all (0 MJ d\(^{-1}\)) and high variability (25 MJ d\(^{-1}\)). Finally, in the ‘onset-of-spring scenario’, we varied the date at which food became available in S2 and S3 from day 0 to day 55 (after 21 March) in steps of 5 days. All parameters were changed independently for each stopover site except for the onset-of-spring scenario where only onsets of spring in S2 and S3 were varied independently.

For each scenario, we predicted staging times on stopover sites and calculated the expected fitness from date and body condition at arrival on the breeding grounds (see Model description). Furthermore, we qualitatively compared the model predictions with empirical data using the ranges of staging times on each site as well as the relations.
between staging times on the three stopover sites. This allowed us to identify potential clues upon which geese base their migratory decisions and to estimate the impact of each parameter on migration schedules and fitness of the geese.

RESULTS

Impact of model parameters on staging times

**Intake rates.** The intake rates at the stopover sites had varying impact on staging times: Departure dates from S1 varied little between day 41 and 44, and these variations rather resulted from changed expected intake rates at the subsequent site(s) than from changes in S1-intake rates itself (Fig. 2A). Predicted staging times in S2 varied between 0 and 12 days, and were mainly caused by both the intake rates on this site and in S3 (Fig. 2B). With increasing intake rates in S3, geese reduced staging times and ultimately avoided S2. In S3, the geese spent between 0 and 16 days, the longest staging periods coinciding with high intake rates in S3 (Fig. 2C).

**Stochasticity.** High stochasticity in food supply on a given site generally decreased staging times on that site but led to an enhanced use of previous or subsequent sites with less stochasticity. For instance, S2 was increasingly avoided when stochasticity on that site was high relative to the stochasticity on S1 and S3 (Fig. 3).

**Onset of spring.** The onset of spring crucially determined staging times on all sites. Geese departed from S1 as soon as spring started in one of the successive sites (Fig. 4A). Staging times in S2 were considerably affected by how much the onsets of spring in S2 and S3 differed (Fig. 4B): In the case where spring in S3 started earlier than in S2 (left part of Fig. 4B), S2 was completely skipped and in contrast, if onset of spring in S3 lagged behind S2, we found long staging times in S2 (right part of Fig. 4B). Staging times on S3 were only determined by the onset of spring in this site (Fig. 4C) with the longest staging times resulting from an early spring and complete skipping resulting from very late springs (day 60).

![Figure 2. Intake rate scenario – Independently varying intake rates in the three stopover sites affected staging times (mean) in S1 (A), S2 (B) and S3 (C) to different degrees. Here, only the impact of intake rates on S2 (x-axis) and S3 (grey boxes) is explicitly shown; the error bars (mean ± SE, whiskers SD) result from varying intake rates in S1. Departure from S1 was only slightly affected by intake rates on this or subsequent site(s). The use of stopover sites S2 and S3 depended on intake rates – the geese preferred the site which offered higher intake rates.](image)
Figure 3. Stochasticity scenario – Day to day stochasticity in food supply was varied from constant (0 MJ d⁻¹) to highly stochastic (25 MJ d⁻¹) conditions. Here, only the case for the impact of stochasticity in food supply on S2 is shown but the results apply to the other sites accordingly. High stochasticity leads to increasing avoidance of the stochastic site (S2, given as mean ± SE, whiskers SD) and longer staging times on sites with comparatively low stochasticity (here S1 and S3).

Figure 4. Onset-of-spring scenario – The onsets of spring varied independently for S2 and S3 from very early (day 10) to very late (day 60). Staging times (mean ± SE, whiskers SD) in S1 (A) were determined by the earliest date at which either of the subsequent sites became available. In contrast, staging in S2 (B) was mostly determined by the difference in onsets of spring between S3 and S2, i.e. an early spring in S3 or a high synchronization of S2 and S3 led to avoidance of S2 whereas longer staging times in S2 resulted from spring in S3 lagging behind S2. Staging in S3 (C) was only determined by the onset of spring at that very location.
Expected fitness
Intake rates on the three sites influenced expected fitness differently. While intake rates in S1 and S2 had only a marginal impact, intake rates in S3 strongly affected fitness (Fig. 5A). Stochasticity at stopover sites did not change expected fitness (Fig. 5B), suggesting that the geese can compensate for non-constant conditions on a particular site by largely avoiding this site (cf. Fig. 3). The onset of spring had a major impact on expected fitness with late springs – notably in S3 – impinging strongly on fitness (Fig. 5C).

Linking model predictions and empirical staging times

Empirical staging times. As a consequence of the limited time available to accomplish spring migration, staging times on the stopover sites were inter-dependent and varied considerably between S2 and S8 days for S1 and 0 and 20 days for S2 (Fig. 6A and 6B). Thus, staging times on S1 determined staging times on the subsequent site S2 but also on S3 such that late departures from S1 reduced staging times on S2 until it was completely skipped when departing later than day 50 (10 May) (Fig. 6A). A similar pattern appeared for the relation between staging times on S1 and S3 – the longest staging times on S3 (up to 18 days) resulted when departing early from S1 (day 36) and the shortest when the geese departed later than day 50 from S1 (not shown). Similarly, staging times on S2 determined how long the geese stayed on S3, a late departure date leading nearly to a skipping of S3 (Fig. 6B). Thus, the departure date from S1 already largely determined how the geese arrange the remaining part of their migration.

Comparing model predictions with empirical staging times. A qualitative comparison of the empirical results with the model predictions reveals a good correspondence. Apart from the intake rate scenario, which aberrantly predicts a positive relationship between staging times in S1 and S3 – the longest staging times on S3 (up to 18 days) resulted when departing early from S1 (day 36) and the shortest when the geese departed later than day 50 from S1 (not shown). Similarly, staging times on S2 determined how long the geese stayed on S3, a late departure date leading nearly to a skipping of S3 (Fig. 6B). Thus, the departure date from S1 already largely determined how the geese arrange the remaining part of their migration.
Figure 6. Interdependent site use in model and reality. Empirical departure times (mean ± SE, whiskers SD) from S1 varied between day 35 and 56, staging times on S2 between 0 and 18 days and on S3 between 0 and 10 days. The use of stopover sites showed a clear interdependence (a): Late departures from S1 shortened staging time on S2 and S3 or similarly, short staging on S2 augmented the staging time in S3. The range of staging times and their relations between sites as predicted by the model scenarios differed substantially. In the intake rate scenario, model predictions covered only a small range of empirical staging times (as indicated by the shaded areas). However, for S3 this looks much more promising. In the stochasticity scenario, staging times were underestimated for S2 and overestimated for S3. For a part of the S1–S2 relation, predictions met reality rather well.
The intake rate scenario had already wrongly predicted a positive relationship between staging times in S1 and S2, but it also predicted a much too restricted range of staging times on S1 (Fig. 6C). Although the stochasticity scenario produced a larger range of staging times than the intake rate scenario, it predicted staging times on S1 and S2 that were too short (Fig. 6E). The only scenario that covered the empirically observed range in the relationship in staging times between S1 and S2 was the onset-of-spring scenario (Fig. 6G).

Similar results were obtained by comparing staging time relations between S1 and S3 (not shown) – again, only the onset-of-spring scenario covered the full range whereas the intake rate scenario covered only a very small section. Although the stochasticity scenario produced a larger range of staging times, it still lacked late staging times for S1 and clearly overestimated S3 staging times.

The relationship between staging times in S2 and S3 were least well reproduced by the scenarios (Fig. 6D,F,H). The predictions from the intake rate scenario resembled the empirical relation, although staging times in S2 longer than 13 days were not found (Fig. 6D). Staging times in S3 were overestimated by both the stochasticity (Fig. 6F) and the onset-of-spring scenario (Fig. 6H).

**DISCUSSION**

We investigated how three aspects of food availability affect spring migration patterns in an arctic-breeding goose species. Our results indicate that the onset of spring is the major determinant for the departure and staging decisions along the flyway. The geese departed from S1 as soon as one of the subsequent sites became available and staging times in S2 depended on the difference in onsets of spring between S2 and S3. This finding supports the suggestion from various field studies on arctic-breeding migratory geese that the geese follow the spring-flush in vegetation development feeding on the highly nutritive early grass (‘green-wave hypothesis’, Drent et al. 1978, Prop 2004, van der Graaf et al. 2006).

However, in contrast to many studies emphasizing the paramount importance of food quantity and quality on stopover sites (e.g. Prop & Deerenberg 1991, Schaub & Jenni 2000, Patterson & Fuchs 2001, Schaub & Jenni 2001), this appeared to be only of minor importance for most of the migration route. This implies that the geese can cope with variation in food quality by adjusting feeding time or intensity (Riddington et al. 1997, Stock & Hofeditz 1997, Therkildsen & Madsen 2000, Hassall et al. 2001) and that in the early stages of migration, geese simply rely on onset of spring whereas in later stages, on the northernmost site, fattening has highest priority (Madsen 2001, Madsen & Klaassen unpubl.).

Furthermore, stochasticity in intake rates was also important in influencing staging decisions. Our results imply that the geese select for low stochasticity whenever possible and attempt to avoid sites with comparatively high stochasticity. Such risk-averse behaviour has earlier been shown to lead to avoidance of the most stochastic sites or to overloads at departure (e.g. Weber et al. 1998).

The model’s predictions in the onset-of-spring scenario corresponded generally well with the observed patterns and ranges in empirical staging times. The range of parameter values used in our study goes potentially beyond those found in reality but this allows us to assess how geese might respond if one or more aspects of food availability change in the future. Such prediction can help to understand the consequences of habitat change – such as those due to changing climatic conditions or land use. Over the past two decades, spring in Western Europe has already advanced by more than two weeks, in some (southern Scandinavian) regions even one month (Høgda et al. 2005). However, during the same period, the onset of spring in northern Europe has remained unchanged or may even have been delayed (Høgda et al. 2005). Our model predicted that Pink-footed Geese react to these changes by departing earlier from S1, staying longer in S2, and not changing staging time in S3, which corresponds well to the changed staging times in the empirical data (Madsen 2001).
However, as well as large scale processes, local human actions may lead to changes in migration schedules. For instance, during 1993–1995 and since 1999, farmers in S3 have organised campaigns to scare the goose flocks off from pastures, where geese and sheep were competing for the early grass. In areas with a scaring regime, goose numbers have been reduced, and among the remaining geese, daily energy intake rates were reduced whilst energy expenditure increased (Madsen 1995). As a consequence, these geese were unable to accumulate sufficient body stores to breed as successfully as geese staying in areas without scaring (Madsen 1995). Such effectively reduced intake rates in S3 were predicted to have a detrimental effect on fitness. However, the geese have partially adjusted to this by reducing their staging time in S3 but, in turn, increased staging time in S2 (Klaassen et al. 2006).

Differences in staging times on stopover sites have usually been attributed to differences in migration strategies, i.e. time minimizing or state maximizing strategies (Farmer & Wiens 1998, Farmer & Wiens 1999, Scheiffarth et al. 2002, Prop et al. 2003). Our results, however, suggest that such a variation between years might just be due to adjustments of migration schedules to variations in environmental conditions of the stopover sites rather than inherently differing migration strategies (Clark & Butler 1999).

REFERENCES


SAMENVATTING
Tijdens de trek wisselen vogels het vliegen af met periodes dat gerust of ‘bijgetankt’ wordt. Beslissingen omtrent de duur van een tussenstop en de afstand dat getrokken wordt, hangen onder meer van de voedselomstandigheden af. Van belang hierbij zijn de opnamesnelheid van het voedsel, de toevallige variatie hierin, en het begin van groei van het voedsel in het voorjaar. De invloed van deze factoren op verblijftijd en fitness van trekvogels werd onderzocht met een rekenkundige techniek die bekend staat onder de naam ‘stochastisch dynamisch modelleren’. Vervolgens werden modelvoorspellingen getoetst met waarnemingen verzameld aan de op Spitsbergen broedende populatie van de Kleine Rietgans Anser brachyrhynchus in de jaren 1990–2002. De rekenkundige modellen gaven aan dat het begin van de voorjaarsgroei van het voedsel het sterkste effect had op het trekpatroon van de ganzen, terwijl de opnamesnelheid van het voedsel veel minder belangrijk was dan verwacht. Naarmate de vogels het broedgebied naderden, werd het belang van opnamesnelheid echter wel groter. Het model voorspelde verder dat de ganzen in staat zijn te compenseren voor een lage beschikbaarheid van voedsel, en dat toevallige fluctuaties in het voedselaanbod geen problemen opleveren. Alleen een lage opnamesnelheid op de laatste tussenstop of een zeer laat voorjaar resulteert in een verlaagde fitness.

De waarnemingen lieten zien dat het gebruik van de ene pleisterplaats effect had op dat van een volgende: de verblijftijden op opeenvolgende pleisterplaatsen waren negatief met elkaar gecorreleerd. De resultaten ondersteunen het belang van een geïntegreerd ruimtelijke model waarin de kenmerken van meerdere pleisterplaatsen worden betrokken om vogeltrek beter te begrijpen.

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