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Articles

Foraging behaviour and fuel accumulation of capital breeders during spring migration as derived from a combination of satellite- and ground-based observations

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The migration strategy of many capital breeders is to garner body stores along the flyway at distinct stopover sites. The rate at which they can fuel is likely to be strongly influenced by a range of factors, such as physiology, food availability, time available for foraging and perceived predation. We analysed the foraging behaviour and fuel accumulation of pink-footed geese, an Arctic capital breeder, at their mid-flyway spring stopover site and evaluated to what extent their behaviour and fuelling were related to physiological and external factors and how it differed from other stopovers along the flyway. We found that fuel accumulation rates of geese at the mid-flyway site were limited by habitat availability rather than by digestive constraints. However, as the time available for foraging increased over the stopover season, geese were able to keep constant fuelling rate. Putting this in perspective, geese increased their daily net energy intake along the flyway corresponding to the increase in time available for foraging. The net energy intake per hour of foraging remained the same. Geese showed differences in their reaction to predators/disturbance between the sites, taking higher risks particularly at the final stopover site. Hence, perceived predation along the flyway may force birds to postpone the final fuel accumulation to the last stopover along the flyway. Flexibility in behaviour appears to be an important trait to ensure fitness in this capital breeder. Our findings are based on a new, improved method for estimating fuel accumulation of animals foraging in heterogeneous landscapes based on data obtained from satellite telemetry and habitat specific intake rates.

Because some animals use stored fat and protein as an important energy source during their migration and breeding, studying their foraging behaviour and fuel accumulation is necessary in order to understand their migratory behaviour (Sapir et al. 2011). Arctic-nesting birds migrating in steps have a limited time to prepare for migration and subsequent breeding because the time window where conditions are suitable at each stopover site as well as for breeding is short (Ankney and MacInnes 1978, Alerstam and Lindström 1990, Prop and Black 1998, Drent et al. 2003). A common migration strategy is therefore to garner body stores along the flyway at distinct stopover sites in order to commence breeding soon after arrival – a strategy called capital breeding (Drent and Daan 1980, Klaassen et al. 2006a). Stopover sites should provide sufficient food to allow for refuelling during their stay (Bauer et al. 2006). However, the optimal foraging conditions for the animals are limited in time and space and therefore the strategy they should employ in order to forage optimally is likely to depend on a range of factors whose importance may vary within a stopover season as well as among different stopover sites along the migratory route.

Foraging behaviour and fuel accumulation of animals can be influenced by physiological factors such as capacity of alimentary tract (as shown to be the case for shrews *Sorex* sp.: Saarikko and Hanski 1990, brent geese *Branta bernicla*: Prop and Deerenberg 1991, Bewick's swan *Cygnus columbianus bewickii*: van Gils et al. 2008). Such digestive constraints may force animals to stop feeding in order to allow the ingested food to pass through the alimentary tract before new food can be ingested (Owen 1972, Saarikko and Hanski 1990, Prop and Vulink 1992, Kersten and Visser 1996). This is likely to be reflected in the amount of time animals spend resting because digestion usually takes place while the animals are resting.

The animals' foraging behaviour and fuel accumulation is also likely to be influenced by environmental factors, for example quality (energetic content) and availability of food (as shown for pink-footed geese *Anser brachyrhynchus*: Madsen 1985a, b; Bewick's swan: Nolet et al. 2002). We generally expect higher fuelling rates if the availability of

highly energetic food increases (as shown for fallow deer *Dama dama*: Focardi et al. 1996, barnacle geese *Branta leucopsis*: Black et al. 2014 and pink-footed geese: Chudzińska et al. 2015).

Foraging behaviour and fuel accumulation can also be influenced by the time available for foraging (both during day and over the entire stopover season, as shown for orange-throated whiptail *Cnemidophorus hyperythrus*: Karasov and Anderson 1984, thrush nightingales *Luscinia luscinia*: Kvist and Lindström 2000, Bewick's swan: Nolet and Klaassen 2005). For some species the amount of accumulated fuel increases if there is more time available for foraging (e.g. thrush nightingale: Kvist and Lindström 2000).

In animals that migrate in steps, the decisions regarding how long to stay and how much fuel to accumulate at each site (Hedenström and Alerstam 1997), which enables animals to maximize the probability of successful breeding, may change from one stopover site to the next. Faster fuelling rates are likely to become more important later in the migration season, because there is less time available to reach the desired amount of energy stores. In order to fuel faster, animals often become more likely to take a risk by spending less time on being vigilant (Bauer et al. 2006, Hedenström 2008, Duriez et al. 2009). Perceived predation risk is more likely to have an impact on the fuelling rates earlier in the migration season.

Fuel accumulation rates of wild animals can be studied using various techniques. Tracking changes in fat stores by observing abdominal profiles (Madsen and Klaassen 2006) or measuring fat content (Schulte-Hostedde et al. 2001) combined with carcass analysis (Ankney and MacInnes 1978, Thomas et al. 1983) provides information on net energy intake rate. However, these methods do not allow for a quantification of metabolisable energy intake and energy expenditure. These variables can be important in order to understand whether the animals' net energy intake is constrained by food availability or by high energy expenditure associated with e.g. disturbance, and hence for evaluating how (for example) altered management, changes in habitat availability, or competition for resources influence the animals' condition. One common method to arrive at separate estimates of metabolisable energy and energy expenditure is to combine three variables: time spent at foraging habitats, food intake rates on these habitats (both necessary for calculating the metabolisable energy intake rate), and time-activity budgets (necessary for estimating energy expenditure) (Merker and Nagy 1984, Bédard and Gauthier 1989, Owen et al. 1992). For animals utilising a single habitat type, whether or not consisting of different patch types, this can be done by making direct observations of individuals or groups (Prop and Deerenberg 1991, Clausen et al. 2012, Gyimesi et al. 2012), but the method is more challenging

when animals utilise a range of different habitats. Here we present a new technique for estimating the net energy intake rate in heterogeneous dynamic landscapes. This technique is based on a combination of satellite tracking data and habitat-specific direct observations of food intake rates and time-activity budgets conducted on randomly chosen flocks of geese, and allows for continuous tracking of the fuelling rates of the studied animals.

In this study we calculate the net energy intake rate (as a measure of fuel accumulation rate) of Svalbard-breeding pink-footed geese in a mid-flyway spring stopover site in mid-Norway. We also study how foraging behaviour and fuel accumulation change along the entire flyway. The aims of this paper are therefore to 1) analyse to what extent fuel accumulation rates of geese in mid-Norway were limited by internal and external factors. We therefore 1.1) investigated to what extent the net energy intake rate was affected by physiological constraints (digestive efficiency) in fuelling rate, 1.2) whether it was related to variations in food availability and 1.3) changes in time available for foraging. 2) We validate our net energy intake rate calculations based on this new technique against calculations derived from changes in the abdominal profile index values of neckbanded pink-footed geese staging at the study site. Finally, 3) we evaluate to what extent geese changed their foraging behaviour and fuel accumulation along the entire flyway. We, therefore, compared 3.1) their fuel accumulation rates; 3.2) time spent resting; and 3.3) reaction to disturbance between all stopover sites along the flyway. A summary of the studied factors and their potential effect on foraging behaviour and fuel accumulation of geese in mid-Norway and along the entire flyway is given in Table 1.

Material and methods

Study population and site

The Svalbard-breeding population of pink-footed geese overwinters in Belgium, the Netherlands and, increasingly, in Denmark. During their migration to the breeding grounds the geese that overwintered in Belgium or the Netherlands stop in Denmark, mid-Norway (in Trøndelag) and north-Norway (in Vesterålen) (Madsen et al. 1999a). The geese start arriving in mid-Norway in early April and numbers peak during late April–early May (Madsen et al. 1999a). Individual geese stay in mid-Norway for an average of 20 d before migrating to north-Norway where they spend on average 4–6 d (Glahder et al. 2006, Bauer et al. 2008b) before migrating to the final destination in Svalbard. Geese commence breeding soon after arrival to Svalbard (Glahder et al. 2006) and therefore depend on the fuel stores (protein

Table 1. Summary of the studied factors and they expected influence on the fuel accumulation (daily net energy intake, DNEI) and foraging behaviour of the satellite tagged pink-footed geese at mid-Norway stopover site and along the entire flyway.

	Constraint	Expected changes in DNEI/goose behaviour
Mid-Norway	Digestive	The interchange of foraging and roosting bouts equally distributed over the day
	Food availability	The higher availability of highly energetic food (stubble, new-sown) the higher DNEI
	Time available for foraging	The longer daylight hours (= time available for foraging) the higher DNEI
Flyway	Distance to breeding area	The closer to the breeding area the higher the DNEI
	Resting time	Less time spent resting and more time spent feeding the closer to the breeding area
	Perceived predation/disturbance	Reaction decreases the closer to the breeding area

and fat) accumulated along the flyway for synthesis of eggs and supporting incubation (Drent et al. 2007).

Since 1990, a total of 3666 individuals have been marked with plastic neckbands, and it is estimated that around 0.8% of the population is currently neckbanded (Madsen unpubl.). Systematic observations of neckbanded individuals are carried out year round along the flyway by experienced observers trained under the same protocol. Information about the body condition of the birds, estimated from visual assessment of the curve of the abdomen (abdominal profile index API); Madsen and Klaassen (2006) is collected in the field whenever possible.

Mid-Norway is semi-mountainous and characterised by a patchwork of agricultural fields and forests. The area is rich with lakes and coastal bays, both of which serve as roost sites for the geese (Fig. 1). Geese are rarely seen resting on the fields and therefore the above-mentioned roosting sites constitute their main resting places (Madsen et al. 1997).

There is, therefore, no difference in resting/feeding behaviour between the habitats (Chudzińska et al. 2013). Roost sites are also the main source of fresh water for geese. Day length increases by 4 h over the stopover season in mid-Norway, and as the geese feed exclusively during daylight hours (Madsen et al. 1997) a corresponding increase in the time available for foraging is expected. Geese are occasionally observed resting on fields in the vicinity of roost sites during nighttimes, however, they do not forage at that time (Madsen et al. 1997). There are four main habitats available to geese: grass (mainly dominated by timothy *Phleum pratense*), barley stubble from the preceding autumn, newly sown/germinating barley grains, and ploughed barley stubble. The geese occasionally forage on waste potato fields. On germinating barley fields geese were only observed foraging on non-germinating grain and not on shoots. Detailed descriptions of each habitat are given in the Supplementary material Appendix 1. These five habitats are henceforth referred to as grass,
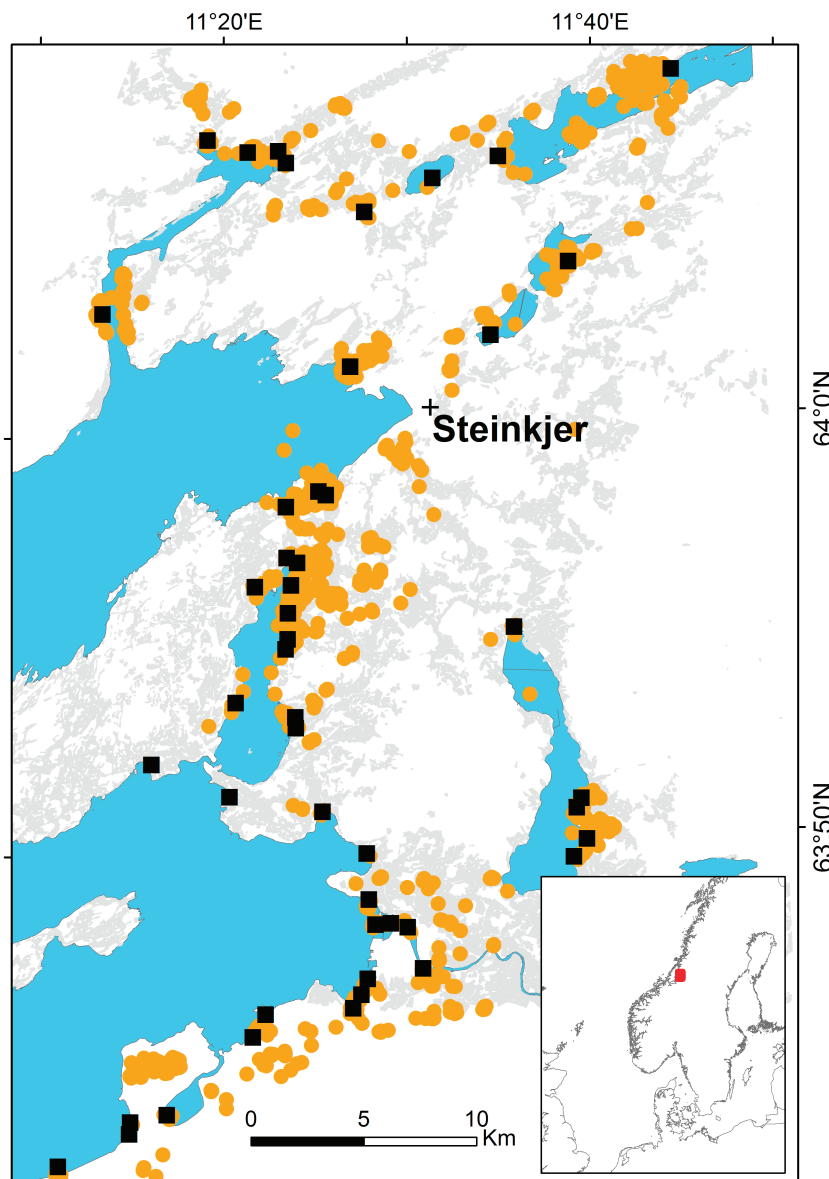

Figure 1. Map of the mid-Norway study area showing all the recorded GPS locations of the 12 geese mounted with transmitters (orange dots). Roost sites are marked with black squares, water with light blue and fields with light grey.

stubble, grain, ploughed and potato. Time-activity budgets for pink-footed geese in mid-Norway revealed that if geese are observed on ploughed fields they mainly rest, however roost sites are their primary resting places (Chudzińska et al. 2013). Grass is widely available during the entire stopover season and it starts growing at the end of April, but is kept short by goose grazing (Bjerke et al. 2014). Stubble fields are gradually ploughed and subsequently sown with barley, which starts germinating in the last part of the stopover season (Madsen et al. 1997).

In order to study whether changes in habitat availability have an effect on fuel accumulation of geese, the entire stopover season was divided into four periods of approximately 8-d. The periods roughly correspond to habitat changes due to agricultural practices. Period 1 refers to 15–25 April, period 2: 26 April–3 May, period 3: 4–11 May and period 4: 12–19 May.

Satellite telemetry

Due to potential interference of satellite antennae during copulation, we chose to tag only males in this study. In 2011, six adult males weighing between 2.55 and 3.20 kg were deployed with satellite transmitters (PTT-100 45 g solar Argos/GPS, Microwave Telemetry, (MT), USA) attached with knicker elastic harnesses (19 g). Geese were caught on 29th March using canon netting in western Denmark (Vest Stadil Fjord: 56.20N, 8.15E). In 2012, five adult males weighing between 2.70 and 3.15 kg were tagged at the same location on 27th March (PTT 40 g solar Argos/GPS, North Star Science and Technology, LLC (NS), USA) using the same attachment and catching methods. Data from two of the five NS tags were not analysed as they only recorded small numbers of positions. However, three of the geese deployed with transmitters in 2011 were still transmitting data in 2012 so a total of 12 yearly data sets from 9 individuals were analysed. We do not treat data from the three individuals which transmitted in the two consecutive years as pseudo replication but as independent data sets because we expect a number of uncorrelated factors in between years (e.g. onset of ploughing season, habitat availability) to occur in mid-Norway. The three individuals did not visit exactly the same locations nor had identical timing in mid-Norway in these two years.

Tags were programmed to record one GPS position every hour between 7:00–20:00 in 2011 and 2012 for MT tags, and between 6:00–19:00 in 2012 for NS tags. At night, the tags were programmed to record a position every two (MT) or four hours (NS). Tags were therefore programmed to record 18 (MT) or 16 (NS) positions per day, and to transmit these to the ARGOS system every second day. Due to poor satellite coverage or low battery power, some tags did not transmit the scheduled number of positions, and on average 12 positions were obtained per day. The number of missing positions did not vary systematically over the day or between the four periods (G-test of contingency: $X^2_{23} = 6.54$, $p = 0.91$; $X^2_{34} = 6.31$, $p = 0.82$, respectively). We calculated energy expenditure and metabolisable energy intake rates using linearly interpolated positions over a 24-h period (detailed descriptions are given in the following

sections and in the Supplementary material Appendix 1). In mid-Norway we received a total of 1711 positions from all individuals and the studied geese stayed 24.7 ± 3.4 d (mean ± SD) at this stopover site.

Externally mounted tags may adversely affect the fuel accumulation of birds by adding mass and increasing drag (Casper 2009, Barron et al. 2010, Pennycuick et al. 2012), but because the transmitters used in this project weighed only around 2% of the body weight of the birds, and because geese spend relatively little time flying during the mid-Norway staging, we expect the additional cost of carrying the transmitters to be negligible. We assessed the potential influence of satellite tags on birds by comparing behaviours of both tagged and randomly chosen non-tagged individuals. We found that there were no differences in behaviour between these two groups (see Supplementary material Appendix 1 for description and full results of that comparison).

Estimation of net energy intake rate as a measure of fuel accumulation rate

Daily net energy intake (DNEI) is the difference between daily metabolisable energy intake (DME) and daily energy expenditure (DEE) (see Supplementary material Appendix 1 for a detailed description of how DME and DEE were calculated). The calculation of DNEI of pink-footed geese was based on three data sets: GPS positions from tagged individuals, because continuous direct observations of the tagged birds were not possible, observations of intake rates of unmarked geese on different habitats, and time-activity budgets based on flock scans. First, GPS tracking allowed us to estimate the minimum distance geese fly, assuming that birds only fly in a straight line between the received positions. In order to calculate the time geese were engaged in flying, we used 50 km h⁻¹ as an average flight speed. This figure was based on readings from instantaneous speed sensors incorporated in the North Star tags, and is comparable with values used in other studies (Green et al. 2002, Fox et al. 2003, Baveco et al. 2011). Only measurements > 20 km h⁻¹ were considered as active flight (Green et al. 2002). Second, GPS tracking provided information about the amount of time geese spent on the different habitats. In combination with information on habitat-specific intake rates (see Supplementary material Appendix 1 for a detailed description of how this intake rate was calculated), this allowed us to calculate DME. Because the distribution of different types of fields changes from year-to-year and within a single stopover season, habitat types were recorded for each of the positions visited by the tagged geese (1–2 d after the date the position was received). The amount of time geese spent on different habitat types was calculated by assuming that a goose spent one (for GPS positions received during the day), two (for GPS positions received from MT tags during the night) or four (for GPS positions received from NS tags during the night) h on the habitat from which the position was received, minus the time necessary to travel from the previous location. Third, we obtained a measure of behaviour of geese in general by conducting 171 half-hour flock scans between 15 April–15 May 2011 in mid-Norway (Chudzińska et al. 2013).

Analysis of foraging behaviour and fuel accumulation of geese in mid-Norway

We analysed the foraging behaviour and fuel accumulation of the tagged birds in mid-Norway in five steps. 1.1) We analysed whether the fuelling rate of the studied pink-footed geese was limited by physiological constraints. Geese foraging on food with low digestibility (e.g. containing a high level of cellulose) may ingest food faster than this food is digested in their alimentary tract, and may therefore be forced to interrupt feeding with resting periods to allow the ingested food pass through the tract. If the DNEI of geese is constrained by their digestive capacity, they are expected to feed as long as it takes them to fill their alimentary tract (time of first passage), and stop feeding or decrease ingestion rate until at least part of the food in the alimentary tract is processed ('digestive break') before the new food can be ingested. Such behaviour has been demonstrated for many species, both birds and mammals (Saarikko and Hanski 1990, Kersten and Visser 1996, Zwarts et al. 1996). We therefore analysed whether foraging bouts of geese (time from one roosting to the next) was comparable to time of the first passage, which has been estimated to be between one and four hours for geese feeding on graminoids (Dorozunska 1963, Marriot 1970, Burton et al. 1979). Next, we investigated whether the resting bouts (time spent on roost site, digestive breaks) was equal to the time necessary for digestion (retention time), which would further support that the geese were limited by physiological constraints. The needed resting time was estimated to be 2 h for grass (Burton et al. 1979) and probably less than 2 h for grain, which is digested faster than grass due to its lower cellulose content (Demment and Van Soest 1985). We assume that geese mainly spend their digestive breaks on roost sites, as they are rarely observed resting on fields in mid-Norway. For the entire analysis, we only took into account resting during daylight, because we assume that roosting behaviour during nights is more related to predator avoidance rather than to digestive breaks. Further, we calculated the correlation (Pearson's product moment correlation) between the length of the feeding bout and the length of the preceding resting bout. We also calculated what proportion of time available for foraging (defined as the hours of daylight between civil twilights (source: Astronomical Applications Department of the U.S. Naval Observatory, < http://aa.usno.navy.mil >) geese spent on roost sites and whether this changed over the stopover season. 1.2) We analysed changes in DNEI in relation to changes in habitat availability by comparing DNEI between the defined periods using a one-way ANOVA. We used Fligner–Killeen test of homogeneity of variance in order to test if there was no evidence of any significant difference in variance across the samples (Conover et al. 2011). 1.3) We studied whether DNEI of geese increased with an increase in time available for foraging by comparing DNEI at the beginning and at the end of the stopover season.

Calculation of the net energy intake rate based on the abdominal profile index

The abdomens of neck-banded pink-footed geese were visually scored during spring migration 2011 and 2012 at all stopover sites, using an abdominal profile index (API) (Madsen and Klaassen 2006). All observations were made by experienced observers trained under the same protocol. In order to assess variations in net energy intake rates in mid-Norway between the four periods, we used only observations of males (because our satellite-tagged birds were males) that had their APIs scored at least twice during the same period (n = 68). For other stopover sites we used data for male pink-footed geese that had their APIs scored at least twice during a stopover season in 2011 or in 2012 (Denmark: n = 52, north-Norway: n = 59). Based on carcass analyses of birds collected along the flyway, Madsen and Klaassen (2006) found a linear relationship between the API values and the energy content of pink-footed geese, with a 6214 kJ change in energy per API unit. To obtain individual DNEI estimates for each bird, the difference between the first and last API scores of a period or season was therefore multiplied by 6214 kJ and divided by the number of days between the scores, as well as by the efficiency for utilisation of metabolisable energy during synthesis (0.80: Lopez and Leeson 2008).

Analysis of foraging behaviour and fuel accumulation of geese along the flyway

In order to get an indication whether foraging behaviour of geese changed between stopover sites we compared 3.1) fuelling rate (DNEI) at the stopover sites calculated based on APIs, as data for intake rates were not available for the other stopover sites. We calculated both daily DNEI as well as net energy intake per 1 h of time available for foraging (expressed as length of daylight) as the time available for foraging differs between the stopovers, and net energy intake per 1h of actual foraging. To calculate time spent on actual foraging, we subtracted the time geese spent on roost sites as well as time spent resting on fields from the available foraging time. In order to estimate DNEI at each stopover site, we calculated the difference between the API score just after arrival and prior to departure from a given site and divided it by number of days between these two observations. As some of the geese stay the entire winter in Denmark, we only analysed observations from this stopover site from March and April, as these months are considered as the start of spring migration (Madsen et al. 1999a). We only analysed observations for which the time interval between these two observations was ≥ 2 d. The conversion from API into kJ was done as described in the previous section. In order to get an estimate of when each goose arrived or left a given site, we only used observations of individuals that were observed at two consecutive stopover sites within 3 d; 3.2) proportion of time available for foraging that geese spent resting calculated based on satellite telemetry data. For Denmark and north-Norway any position taken on water was considered as spent on a roosting site because in these two stopover sites roost sites are not as clearly defined as in mid-Norway, and geese are observed roosting on a variety of water reservoirs. As in case of mid-Norway, one GPS position on water of a tagged bird was considered equal to one hour spent at such place. Time geese spent resting when they were on foraging fields was based on previous studies (see caption for Fig. 5). We compared 3.3) the distance at which geese reacted to disturbances based on literature

search (see caption for Fig. 5). In these studies, the distances at which geese reacted to disturbances were measured as a distance from which flocks take flight estimated using a car as a standard stimulus triggering escape flight. The flight distance was estimated to nearest 5–25 m depending on the study.

The results are shown as mean ± SD unless otherwise indicated. All statistical analyses were performed in R 3.1.0 (R Development Core Team).

Data available from Movebank Data Repository: project id: 49535504, <www.movebank.org>.

Results

Analysis of foraging behaviour and fuel accumulation of geese in mid-Norway

Calculation of net energy intake rate and evaluation of physiological constraints. Factors affecting daily energy expenditure

The average daily metabolisable energy intake (DME) was 4.6 times BMR and the average daily energy expenditure (DEE) was 2.2 times BMR. Time spent on roost sites and in transit made the greatest contributions to the daily energy expenditure, DEE (roost: 33 ± 9%; flying: 14 ± 8%). Thermoregulatory costs constituted only 3 ± 1% of DEE. Based on flock scans conducted in 2011 (Chudzińska et al. 2013) and Supplementary material Appendix 1, Eq. A5 energy expenditure did not differ among field habitats (ANOVA: $F_{3,119} = 0.18$, p = 0.09) nor between field habitats and roost sites (geese are involved in various activities while at a roost site like preening, walking and swimming), and energy expenditure was on average 54.28 ± 1.47 kJ h^{-1} (n = 49; one-way ANOVA, $F_{2,46} = 0.88$, p = 0.42). The average daily net energy intake (DNEI) for the tagged pink-footed geese during their stay in mid-Norway was 1706 ± 351 kJ d^{-1} (mean ± 1 SD). This is equivalent to 2.4 times BMR (as calculated based on equation by Lasiewski and Dawson (1967), see Supplementary material Appendix 1 for more details),

and resulted in an average body mass increase of 49 ± 10 g d^{-1}; or 2 ± 0.01% of lean body mass (LBM) d^{-1} (LBM = 2.47 kg for a male pink-footed geese by Madsen and Klaassen (2006)). The average total net energy intake rate obtained by the tagged geese over the entire stay in mid-Norway was 2.36 ± 1.36 MJ, resulting in an average body mass increase of 685 ± 395 g. This corresponds to a 24 ± 14% increase in goose body mass from that measured on the day of tagging (28 ± 16% increase from the lean body mass).

The mean length of foraging bouts for geese was 4.2 ± 4.9 h, which is close to the upper limit of the first passage time (4 h). The mean length of resting bouts was 2.2 ± 1.7 h, close to the estimated retention time (2 h). Overall, there was no significant correlation between the length of the foraging bout and the length of the preceding resting bout (Pearson's correlation: p = 0.07, DF = 243, r = 0.12). Such correlation was also not observed for any individual separately (for each individual p > 0.09).

Changes of fuel accumulation rate in relation to time available for foraging

The tagged geese spent most of their time at roost sites during the night and around noon, regardless of the period (Fig. 2). Geese headed for the fields shortly before the beginning of the morning civil twilight, and returned to night roost sites after the commencement of the evening civil twilight. For all periods combined, the average amount of time spent on day roosts was 6.28 h d^{-1}. Time spent on day roosts, expressed as the percentage of time available for foraging, did not change between the periods (ANOVA: $F_{3,29} = 1.55$, p = 0.22; Fig. 3A). The overall time spent on roosts during the entire day (i.e. time on day and night roost summed) decreased as the season progressed (Fig. 3B).

Changes in DNEI in relation to changes in habitat availability and comparison of DME between field habitats

Geese were mainly foraging on stubble fields during the first period, on grass during the second and third, and on grain during the final period (Fig. 3B). The tagged birds rarely foraged on waste potato fields (less than 1% of the foraging
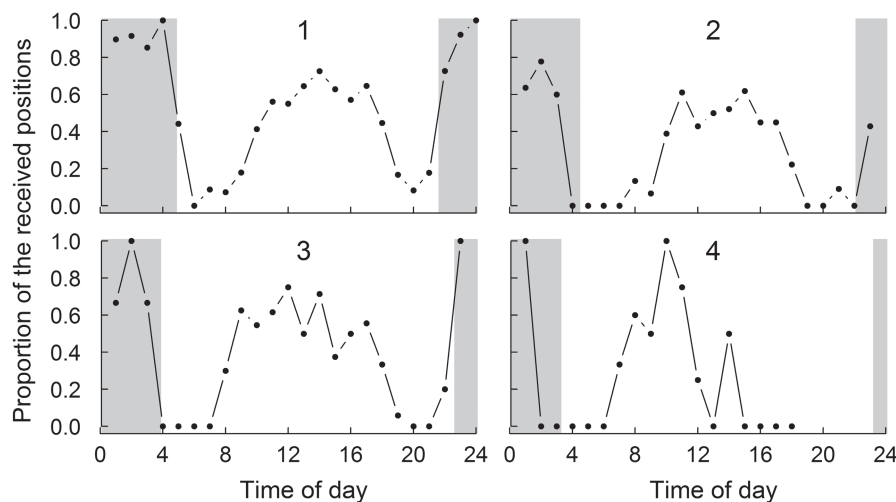

Figure 2. Diurnal changes in the proportion of GPS positions received from the roost sites for the four periods (p1: n = 12; p2: n = 7; p3: n = 9; p4: n = 2) from 12 pink-footed geese during spring migration at the mid-Norway stopover site. Shaded areas indicate night, defined as the time between civil twilights.
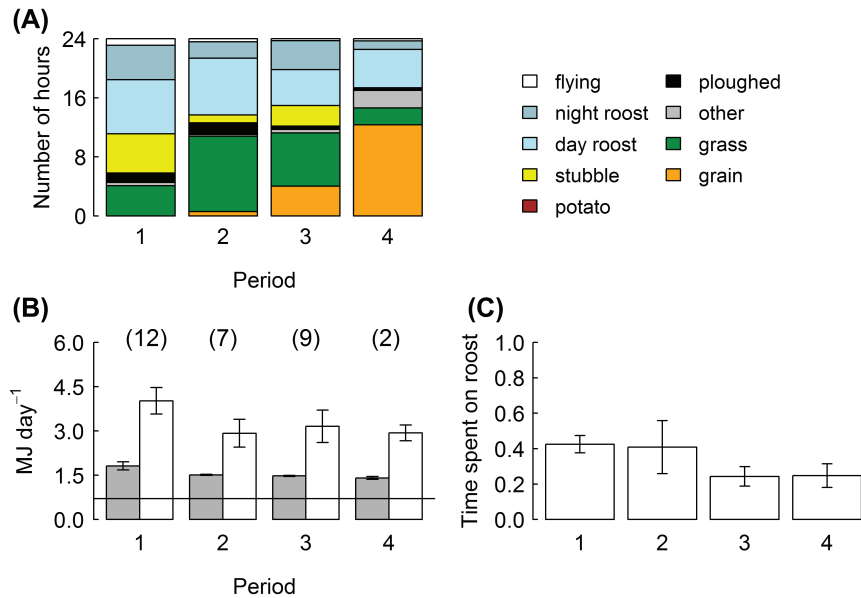
Figure 3. (A) The daily distribution of time spent on different field habitats, at day and night roost sites, and flying for pink-footed geese staging in mid-Norway during spring migration. 'Other' refers to habitat types that cannot be classified as one of the already defined types (e.g. snow, positions taken during flying), (B) the daily energy expenditure (grey bars) and daily metabolisable energy (white bars) for the four periods (mean ± 1 SE). The numbers in parentheses indicate the number of birds transmitting during the respective period. The horizontal solid line indicates mean BMR. (C) The proportion of daylight hours (i.e. hours available for foraging) spent at day roost sites for the four periods (mean ± 1 SE).

time), and in general only during the first half of the season (due to very small size of the bars, these results are not visible in Fig. 3B). Over the course of the season the average amount of time per day spent in transit (flying) decreased. There was neither diurnal nor periodical pattern in habitat selection of the studied geese and all of the tagged geese used most of the available habitat types every day, however in different proportions (Fig. 3B).

Neither DEE nor DME differed significantly between periods (one-way ANOVA, $F_{3,26} = 2.74$, p = 0.06; $F_{3,26} = 1.08$, p = 0.38, respectively) (Fig. 3C).

Feeding on stubble fields resulted in a metabolisable energy intake rate of 559.0 kJ h^{-1}, whereas feeding on grass and newly sown fields resulted in obtaining comparable amounts of metabolisable energy (191.4 kJ h^{-1} and 201.6 kJ h^{-1}, respectively). Potato was the most profitable habitat type (879.5 kJ h^{-1}), but due to the small sample size used to calculate the caloric value of that habitat type, the result should be treated with caution (Supplementary material Appendix 1, Table A1). However, geese never spent more than 0.5% of their daily time on potato fields, therefore, this habitat did not have a significant influence on DNEI.

Calculation of the net energy intake rate based on the abdominal profile index

During their stay in mid-Norway geese showed an increase in API with an average increment of 0.30 ± 0.06 API d^{-1}, which equals a DNEI of 1871 ± 413 kJ d^{-1}; 54 ± 12 g d^{-1}, or 2 ± 0.01% LBM d^{-1} (2.7 BMR) (no data were available for period 4). The satellite telemetry and time-activity budget-based values of DNEI were on average 8% lower than the API-based values of DNEI (Fig. 4). Similar to results obtained from telemetry and time-activity budgets, DNEI

values based on API did not differ between the periods (one-way ANOVA, $F_{1,67} = 0.25$, p = 0.62) (Fig. 4).

Analysis of foraging behaviour and fuel accumulation of geese along the flyway

Changes on fuel accumulation rate along the flyway
The DNEI obtained by pink-footed geese increased along the flyway with lowest DNEI obtained in Denmark (0.94 ± 0.41 MJ d^{-1}; 1.34 BMR) and highest in north-Norway (2.72 ± 0.82 MJ d^{-1}; 3.83 BMR). DNEI increased by 50% from

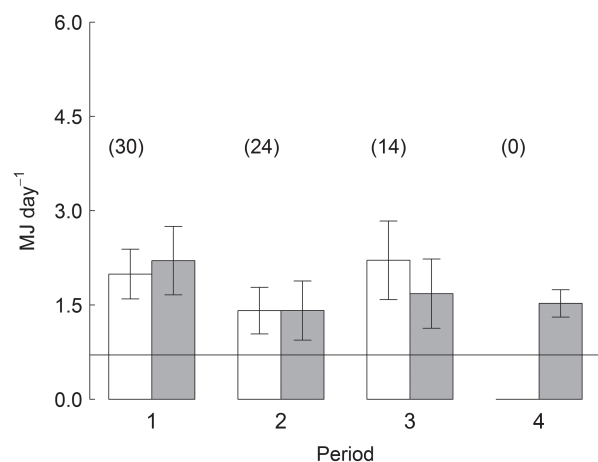Figure 4. Daily net energy intake rate of pink-footed geese staging in mid-Norway based on satellite telemetry and time activity budgets (grey bars) and on abdominal profile index (API, white bars) for the four periods. The numbers in parentheses indicate the number of individuals that the API-based values were calculated from; no API data were available from period 4. The horizontal solid line indicates mean BMR.

Denmark to mid-Norway and by 45% from mid-Norway to north-Norway (Fig. 5A). The DNEI in Denmark, mid-Norway and north-Norway were significantly different (ANOVA: $F_{2,177} = 18.03$, $p = 0.02$). However, net energy intake obtained per 1 h of time available for foraging and per 1 h of actual foraging did not differ between the stopover sites (ANOVA: $F_{2,177} = 0.52$, $p = 0.6$; $F_{2,177} = 0.05$, $p = 0.9$, respectively; Fig. 5B).
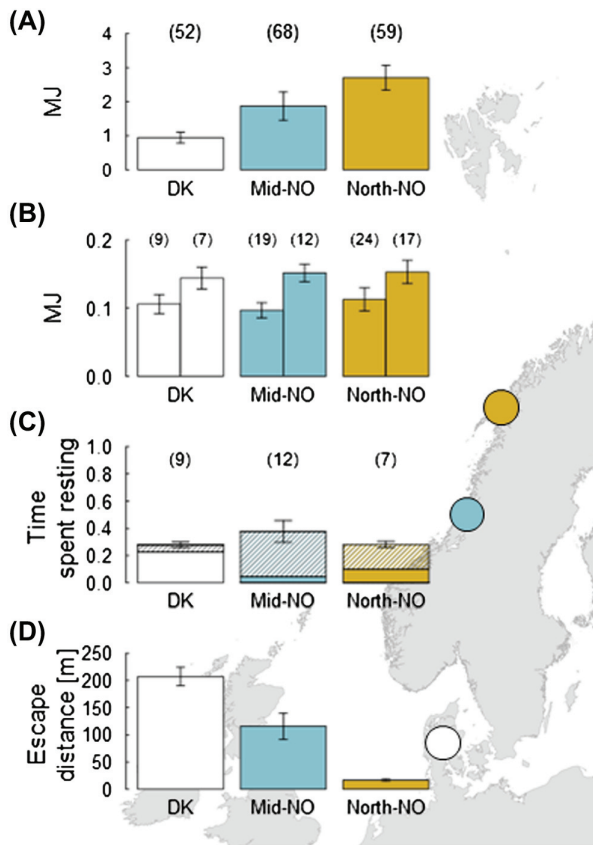

Figure 5. Summary of energetic and foraging behaviour of Svalbard-breeding pink-footed geese along the spring migration flyway. (A) Daily net energy intake for three stopover sites estimated from changes in abdominal profile index (API) (mean ± 1 SE). The numbers in parentheses indicate the number of individuals that the API-based values were calculated from. The average time the API-scored geese spent at each stopover site was 10.8, 18.8 and 2.6 d, respectively; (B) net energy intake (NEI) estimated from changes in API per 1 h of time available for foraging (left bar). Average length of daylight time is indicated on top of the bars. Right bars show NEI per 1 h of actual feeding. Average length of time spent feeding during day is indicated on top of the bar. The error bars show mean ± 1 SE, (C) the proportion of time available for foraging geese spent resting. The lower bars for each stopover site indicate the proportion of time geese spent resting on fields based on data from literature (DK: Madsen (1985a), mid-NO: Chudzinska et al. (2013), north-NO: Madsen unpubl.). The upper bars filled with matching colours hatched pattern show time geese spent resting on roost sites (mean ± 1 SE) estimated from GPS tagged pink-footed geese. The numbers in parentheses indicate the number of birds transmitting at each stopover site; (D) changes in response to perceived predation risk along the flyway (using the distance at which goose flocks fled in front of an approaching car as a standard) DK: Madsen (1985b), mid-NO: Madsen unpubl., north-NO: Madsen (1998).

Changes in time spent resting and the effect of disturbance on geese along the flyway

Expressed as the overall proportion of time potentially available for foraging, geese did not differ between stopover sites in the time spent resting (ANOVA: $F_{2,180} = 26.01$, $p = 0.04$, Fig. 5C). The proportion of time available for foraging which geese spent on roost sites was the highest in mid-Norway (33%) and lowest in Denmark (5%) (Fig. 5C). Geese in mid-Norway spent less time resting in the fields than at other stopover sites (Fig. 5C). The distance at which geese fled as a reaction to disturbance decreased along the flyway (Fig. 5D).

Discussion

Capital breeders migrating in steps face a number of decisions on their journey, such as how long to stay and how much fuel to accumulate at each site. Here we demonstrate how such decisions, that are often crucial to the birds' breeding success, can be determined by a variety of internal and external factors having an influence on birds' fuel accumulation within a stopover season as well as along the flyway.

Superficially, the results suggest that the fuelling rate of geese and especially metabolisable energy intake rate in mid-Norway can be limited by digestive constraints. On average geese foraged on fields until their alimentary tracts were filled. Then they flew to the roost sites and stayed there as long as necessary to digest. However, we observed large variations in the duration of foraging and resting bouts, which is inconsistent with the hypothesis that fuelling rates are limited by digestive constraints, as such constraints would cause foraging to be spread more evenly over the day since animals have to take a rest every time their alimentary tract is full (Saarikko and Hanski 1990, Zwarts and Dirksen 1990, Bednekoff and Houston 1994). In the present study foraging usually only decreased around midday when the geese went to the roost sites. Our results could still support the hypothesis that fuelling was limited by digestive constraints if the geese spent time digesting on fields rather than on the roost sites. This was, however, not the case in mid-Norway and we therefore conclude that digestive constraints were not the major factor limiting the daily net energy intake (DNEI).

Predation and human disturbance (which can also be regarded as a perceived predation risk (Gill et al. 1996, Tombre et al. 2005, Klaassen et al. 2006b)) may reduce the foraging time of birds and therefore the amount of accumulated fuel by forcing birds to spend more time in a predator/disturbance safe resting place instead of at a foraging area (Ely 1992, Fransson and Weber 1997). In mid-Norway, geese are only occasionally hunted by white-tailed eagles *Haliaeetus albicilla* (Madsen et al. 1998), but human disturbance occurs frequently in the study area (Chudzińska et al. 2013). Such disturbance could therefore be the main reason why geese spent up to 43% of the time available for foraging on predator and disturbance safe roost sites. Ely (1992) showed that white-fronted geese *Anser albifrons* were more likely to spend extensive periods of time at roost sites (up 65% of daylight) if the risk of predation was high in foraging areas. Mid-Norway has been used by geese only in recent years,

from late 1980s. Before this time goose flocks passed this area and continued along the west coast to north-Norway, where they were primarily observed foraging on salt marshes and pastures fringing the sea (Rikardsen 1982, Madsen et al. 1997). Arable landscapes offer a readily accessible and highly nutritional food source which has led to an apparent increase in the use of pastures and agricultural crops by a variety of species (e.g. roe deer *Capreolus capreolus*: Cibien et al. 1989, various goose species: Madsen et al. 1999b, Fox et al. 2005, buff-breasted sandpiper *Tryngites subruficoloos*: McCarty et al. 2009). However, foraging in agricultural landscapes results in a higher exposure to human presence compared to more natural and remote areas, which can greatly influence foraging behaviour of birds (such as geese as in this study), but also of mammals (e.g. roe deer: Hewison et al. 2001). Other studies conducted in mid-Norway also demonstrated that human disturbance had an influence on foraging behaviour and habitat selection of pink-footed geese. Chudzińska et al. (2013) showed that a larger proportion of geese fed under undisturbed than disturbed conditions, and Chudzińska et al. (2015) demonstrated that geese preferred to forage in areas farther away from disturbance sources.

The results suggest that the DNEI of geese staging in mid-Norway may be limited by habitat availability. However, this limitation can be counteracted by an increase in time available for foraging associated with an increase in day length. At the beginning of the season the geese foraged on energy-rich stubble fields that allowed them to accumulate enough energy even though the time available for foraging was short. At the end of the stopover season, geese still accumulated almost the same amount of energy, probably due to the fact that the most abundant habitat types were of lower energetic value than at the beginning of the season, but day length and therefore time available for foraging had increased.

Animals using stepwise migration face a number of decisions on their journey and their successful migration depends on these decisions taken along the flyway (Hedenström and Alerstam 1997). We would therefore expect the amount of accumulated fuel to reflect a trade-off between maximising this amount and other motivations like minimising predation risk, optimising the time of arrival to the breeding grounds and optimising the fuel rate according to the amount of time left to the onset of breeding. As the latter factor changes significantly along the flyway, faster fuelling rate are likely to become more important later in the migration season. Contrary to these expectations, although daily energy intake of pink-footed geese increased significantly along the flyway, this increase is likely to be primarily a function of the increase in daylight hours, and, hence, time available for foraging. The amount of energy accumulated by geese per hour of time spent foraging did not change between the stopover sites. At the same time geese considerably changed their resting behaviour along the flyway. Although the overall amount of time which geese spent resting did not vary between the stopovers, only in mid-Norway geese spent this time on the roost sites during day, and as shown by the results this behaviour shows clear diurnal variation and is not only a function of digestive constraints. At each stopover site geese show diurnal changes in foraging behaviour: geese in Denmark and mid-Norway

have their peak in foraging activity in the morning and afternoon (Madsen 1996, Therkildsen and Madsen 2000, Chudzińska et al. 2013, this study). In north-Norway, where the sun does not set during the summer, such peaks are not clearly defined (Madsen 1998). In Denmark and in north-Norway geese are more likely to take a rest while foraging on fields rather than going back to a predator safe roost site. In Denmark there are numerous places where geese can forage or rest relatively undisturbed (nature reserves, large fields), whereas in mid-Norway all foraging areas are close to roads and settlements. The reaction to disturbance is also reflected in the escape distance. Geese in Denmark react to a disturbance event at a longer distance than geese in mid-Norway, and geese in north-Norway flee when a source of disturbance is very close. They are also more likely to return faster to a foraging patch from which they were disturbed (Madsen 1998). We therefore conclude that predator/disturbance avoidance is probably an important factor shaping foraging behaviour of geese at each stopover site, however and according to expectations, further north along the flyway, when less time is available to the onset of breeding, geese are more likely to undertake a more risky behaviour in order to obtain a desired energy intake, a behaviour also shown for other species (Lima 1986, Madsen 1998, Lima and Bednekoff 1999, Duijns et al. 2009). In the light of predation risk being mass specific (Lima 1986, Gentle and Gosler 2001), geese in mid-Norway may not fuel to their maximum level but instead postpone the final fuel accumulation to the last stopover site. This is in accordance to the model predictions by Bauer et al. (2006). However, as shown by this model, declining intake rates at the last stopover site due to stochastic events clearly decreased fitness of geese, indicating that such behaviour may be risky.

The DNEI values based on satellite tracking data and time-activity budgets were comparable to those based on API. Overall we conclude that the method described in this study is a recommendable way of estimating net energy intake rate. It is unique in being the only method currently available that makes it possible to obtain the ratio between daily metabolisable energy (DME) and daily energy expenditure (DEE) for species utilising different habitats within a stopover site. Population-level survey, on the other hand, would not allow us to calculate in details energetic of geese, as keeping track of the same individuals is very difficult. Our method allows evaluating whether any changes in energy budget of an animal are due to changes in DEE or DME. Such knowledge may have great management implications. For example, an increase in human disturbance at the study area may force birds to take-off more often and fly longer distances resulting in an increase in DEE. Being able to calculate both DEE and DME allows us to study whether birds would be able to compensate high flying expenses by increasing their DME by foraging more intensively and/or increase their foraging activity on more energetic habitat type. The new approach presented here is quite labour intensive, but allows for almost continuous tracking of DNEI which gave an insight into changes in DNEI both within a day and between days, a result difficult to obtain based on API due to its low time resolution. We assumed that the obtained GPS positions accounted fully for the movement of the tagged birds, and also that they took the most direct flight path when moving

between locations, thus travel distances are likely to have been underestimated. Doubling the amount of time geese spent in transit led to an 11% decrease in DNEI and therefore a value 19% lower than DNEI estimation based on API. Energy expenditure estimates based on GPS with the current resolution should therefore be treated with caution. Several factors that are known to influence DME were not taken into account in this study. Feeding intensity and intake rate of flock animals are known to be related to flock status and density of birds in flocks (Black et al. 1992) and these factors were not taken into account in this study. Future accounting for the uncertainties related to the above-mentioned issues may improve our method of estimating DNEI.

We conclude that digestive constraints were not the main factor limiting fuel accumulation rates of geese in mid-Norway. Their fuelling rates were limited by habitat availability, but this limitation was counteracted by an increase in time available for foraging and geese were therefore able to maintain a constant level of net energy intake throughout the stopover season. Geese increased their daily net energy intake along the flyway; this increase was primarily related to the increase in time available for foraging while net energy intake per hour remained the same. Geese, however, showed differences in reaction to predator/disturbance and these differences shaped geese foraging behaviour by forcing them to spend more time in undisturbed places (roost sites) and hence disrupting their foraging. Predator/disturbance avoidance is another important factor that can influence foraging behaviour of geese along the flyway. Changes in perceived predation along the flyway may force birds to postpone the final fuel accumulation to the last stopover along the flyway. We also showed that geese adjust their foraging behaviour to the conditions they meet at each stopover site. Such flexibility in goose behaviour is in line with the suggestions by Bauer et al. (2008a) and Duriez et al. (2009) that decision rules that control when geese leave the stopover sites change during the course of migration for pink-footed geese. Other studies also show flexibility in pink-footed geese stopover foraging and fuelling behaviour in response to food availability and inter-specific competition (Clausen and Madsen 2015, Madsen et al. 2015), and winter harshness (Clausen et al. 2015). Such flexibility has been also predicted for similar species by modelling (Weber et al. 1998) and also demonstrated for e.g. Bewick's swans (Beekman et al. 2002), barnacle geese (Drent et al. 2007) and pectoral sandpiper *Calidris melanotos* (Farmer and Wiens 1999). Understanding flexibility in birds' behaviour as well as interconnectivity and importance of each stopover site are important for the flyway management of populations and in identifying critical habitats along the migratory routes (e.g. The Critical Site Network Tool developed by Wetlands International; < http://wow.wetlands.org/ >). (Madsen 1985b).

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Supplementary material (Appendix JAV-00899 at <www.avianbiology.org/appendix/jav-00899>). Appendix 1.