Body stores persist as fitness correlate in a long-distance migrant released from food constraints

Adriaan M. Dokter, Wimke Fokkema, Steven K. Bekker, Willem Bouten, Barwolt S. Ebbinge, Gerard Müskens, Han Olff, Henk P. van der Jeugd, and Bart A. Nolet

Centre for Avian Migration and Demography, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB, Wageningen, The Netherlands; Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB, Wageningen, The Netherlands; Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE, Amsterdam, The Netherlands; Conservation Ecology, University of Groningen, P.O. Box 11103, 9700 CC, Groningen, The Netherlands; and Team Animal Ecology, Wageningen Environmental Research (Alterra), Wageningen University, P.O. Box 47, 6700 AA, Wageningen, The Netherlands

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INTRODUCTION

Long-distance migratory birds rely on the acquisition of body stores to fuel their migration and reproduction. Breeding success depends on the amount of body stores acquired prior to migration, which is thought to increase with access to food at the fueling site. Here, we studied how food abundance during fueling affected time budgets and reproductive success. In a regime of plenty, we expected that 1) limitations on food harvesting would become lifted, allowing birds to frequently idle, and 2) birds would reach sufficient fuel loads, such that departure weight would no longer affect reproductive success. Our study system comprised brent geese (Branta b. bernica) staging on high-quality agricultural pastures. Fueling conditions were assessed by a combination of high-resolution GPS tracking, acceleration-based behavioral classification, thermoregulation modeling, and measurements of food digestibility and excretion rates. Mark-resighting analysis was used to test for correlations between departure weight and offspring recruitment. Our results confirm that birds loafed extensively, actively postponed fueling in early spring, and took frequent digestion pauses, suggesting that traditional time constraints on harvest and fueling rates are absent on modern-day fertilized grasslands. Nonetheless, departure weight remained correlated with recruitment success. The persistence of this correlation after a prolonged stopover with access to abundant high-quality food, suggests that between-individual differences in departure condition are not so much enforced by food quality and availability during stopover, but reflect individual quality and longer-lived life-history traits, such as health status and digestive capacity, which may be developed before the fueling period.

Key words: arctic waterfowl, carry-over effects, cultivated grassland, GPS tracking, migratory fueling, recruitment.

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referred to as “prisoners of their food supply” during premigratory staging (Drent and Prins 1987; Zwarts 1990), because they rely on a seasonal increase in food availability for putting on the fuel that is required to “escape” towards their breeding grounds. Resource and time limitations also lead to competition between individuals, a process that can enforce individual differences in accumulated body weight observed before migratory departure (Teunissen et al. 1983; Prop and Deerenberg 1991; Black et al. 1992; Inger et al. 2010). Fueling may also occur in a regime of food abundance rather than scarcity, such as in specific natural habitats (Tsipoura and Burger 1999), but especially when birds are able to capitalize on resources provided by human activity. Pastures have become a major foraging ground in winter and spring of wild goose populations and are currently the main spring fueling habitat of most arctic-breeding species in western Europe. Increases in both grass quality and availability at staging sites through widespread use of artificial fertilizers (Vickery 1994; Van Eerden et al. 2005) are considered major drivers of population growth of wild geese (Fox et al. 2005; Fox et al. 2017). Fueling on man-made habitats also includes pastures for ducks (Owen and Williams 1976) and plowers (Gillings et al. 2007), orchards for songbirds (Rey 2011), and rice and corn fields for waders and waterbirds (McLandress and Raveling 1981; Güzman et al. 1999; Abraham et al. 2005; Gauthier et al. 2005; Lourenço et al. 2010). These habitats can be suitable replacements for lost natural staging habitats, especially when additionally managed for wildlife and may even provide food that is more easily accessible compared with remaining traditional habitats (Gauthier et al. 2005).

Systems with abundant food provide interesting case studies for evaluating the effects of food availability on time budgets, departure conditions, and breeding success. When food is plentiful, we predict foragers to be able to collect food rapidly and efficiently, such that time constraints become lifted. Animals are expected to frequently loaf and rest, as they have more available time than needed for foraging (Jeschke and Tollrian 2005). During active fueling periods, we also expect animals to take frequent digestion pauses (Kersten and Visser 1996), as collecting food will take less time than digesting it. Animals are further expected to be able to reach the fuel loads they require, such that fueling-related carry-over effects of departure condition into the breeding season will be absent.

We studied these issues in the dark-bellied brent geese (Branta h. bernicla, hereafter brent geese), staging on the agricultural grasslands of the island Terschelling in the Dutch Wadden Sea, in April/May prior to departure to their breeding grounds. These migrants need to accumulate large body stores not only to fuel their 4500 km migration to the Russian arctic, but as a capital breeder also for egg formation and incubation (Ankney 1984; Klaassen et al. 2006; Spaans et al. 2007). Female brent geese that were heavier at the onset of spring migration were more likely to return with offspring in autumn than females departing with fewer stores (Ebbinge 1989; Ebbinge and Spaans 1995), suggesting an active carry-over effect from the fueling stage into breeding stage.

The vast majority of the population of dark-bellied brent geese breed in the Russian high arctic of the Taimyr peninsula; therefore, migration distances are long and of comparable length across individuals. Birds winter along the coasts of western Europe, where many birds feed on eelgrass beds in autumn and winter (Ganter 2000), before switching to terrestrial resources when marine resources are eaten out (Inger et al. 2010). Fueling in spring occurs predominantly on agricultural grasslands. During fueling, geese occupy only a limited area of available grasslands, which they graze repeatedly to keep the grass in a young nutritious state (Bos et al. 2004).

To test whether these grasslands indeed represent a regime of food abundance that induces loafing and inactivity, we equipped geese with novel high-resolution GPS tags and accelerometers that can monitor individual time budgets in high detail. Field observations and a food-sampling program were used to determine ingestion rates, digestive throughput, resource quality, digestibility, and thermoregulation. All data were combined into fueling simulations that reconstructed the birds’ fueling trajectories, which were used to rank factors affecting the birds’ mass increase through a sensitivity analysis.

If constraints associated with food on spring fueling and maintenance of winter body stores are no longer present, brent geese are expected to be able to reach fuel loads sufficient for successful migration and subsequent breeding. As a result, the correlation between reproductive success and departure weight, as found 3 decades ago for dark-bellied brent geese (Ebbinge 1989; Ebbinge and Spaans 1995), may have disappeared on the intensively managed grasslands. This correlation is tested by a mark-resighting analysis of a long-term color ringing scheme.

**MATERIALS AND METHODS**

**Tracking details and study site**

The study area was located in the Dutch Wadden Sea, on the barrier island Terschelling (53.38 N, 5.29 E). The southern half of the island consists of 14 km² contiguous agricultural grasslands, which are managed as a goose fueling reserve without any scaring practices or hunting. Fields at the southern end of the island are used intensively by brent geese for grazing, and roosting occurs on the mudflats directly opposite to the sea dike. We tagged 21 male brent geese in spring 2012 with UvA-BiTS GPS trackers (Bouten et al. 2013), which were attached as a backpack using nylon strings inserted in 4 mm wide silicon tubing. We selected males for carrying transmitters because males are the larger sex and presumably less affected by the added weight. Trackers were set to collect GPS fixes every hour down to every 5 min depending on available solar power. Following each GPS fix, we collected 7 measurements at 20 Hz of tri-axial accelerometer data to quantify the bird’s activity (see Supplementary Material). Eleven birds were contacted at the catching site after the breeding season, of which 7 birds returned for migratory fueling in spring 2013, the focal year of this study. Six of these birds had a functional tag and form the basis of the analyses.

The accelerometer data were used to distinguish inactivity (resting) from active behavior (verified with camera observations of GPS-tagged captive birds, see Supplementary Material); within active behavior, flying, with its characteristically high acceleration variation (Shamoun-Baranes et al. 2012), was scored separately. Combining accelerometer activity (see Supplementary Table S1 and Supplementary Appendix S2), location, and time of day, we classified GPS fixes into 12 categories: flying, pasture active, mudflat active, on water (using a tidal reconstruction), pasture resting, and mudflat resting, each split out by day and night. For each individual, daily time budgets were quantified as the daily proportion of time spent in each category.

Temporal trends in time budgets were analyzed using a linear mixed model for each time budget category, using the lme function of R-package nlme (Pinheiro et al. 2018). We considered date as fixed effect, and individual as random intercept effect, as in activity ~ date + (1 | ID). The significance of the date effect was tested using a likelihood ratio test against a constant null model. Coefficients are reported for a fit by restricted likelihood maximization (REML).
Mark-resighting analysis

Adult brent geese were captured yearly at the study site by canon netting in the period 13–21 May from 2010 to 2016, that is, 1–2 weeks before departure at the end of May, with each year having 1–2 catches within 3 days (see Supplementary Table S2). Individuals were color-ringed with unique codes, and weighed within a few hours after capture. The study site was visited almost daily by field observers from October to May, who noted down color ring codes and number of juveniles accompanying adult birds. All observations were stored and accessed from the geese.org database, a public platform where observations of individually marked waterbirds can be submitted. We took the largest number of juveniles observed in a family within a winter season as the estimate of recruitment, since juveniles may separate from their parents over the course of spring. We calculated a scaled mass index (Supplementary Appendix S3), using standardized major axis (SMA) regression on head and wing length to correct for structural size differences between individuals, following Peig and Green (2009). SMI was used in statistical inferences, but we show uncorrected masses.

Sampling of food and excreta

Grass and excreta were sampled on 27 fields organized in multiple transects of increasing distance to the intertidal (see Supplementary Figure S1), such that fields exposed to different grazing intensities were included in the program. On each field, a 1-m² exclosure was put in place on 13 March 2013, which was moved by several meters into a new position during field visits every 2 weeks. Plant material was collected from inside the exclosure on 26 Mar, 10 April, 21 April, 8 May, and 21 May. During each field visit, we quantified grazing pressure per field (in droppings/m²) by counting droppings in 5 circles of 4 m², which were cleared each visit and of which the centers were marked by inconspicuous 5-cm protruding sticks. From each circle, 2 droppings were collected as fresh as possible. To measure vegetation height in each circle and inside the exclosure, we used a light 25-cm diameter disc that could slide over a vertical ruler until resting on the top of the vegetation. Grass and droppings were oven-dried at 60 °C for 24 h directly after collection. Plant and dropping material was ground through a 1-mm sieve, after weighing droppings individually. A random selection stratified by period yielded 50 samples (25 grass and 25 excreta), which were chemically analyzed for acid detergent fiber (ADF) (Van Soest et al. 1991), ash content, and energy content 𝑢 (using an IKA C5000 oxygen bomb calorimeter). The chemical ADF analyses were used as a calibration dataset for estimating ADF concentrations of the full dataset (135 plant samples, 117 excreta samples) by near-infra-red reflectance spectroscopy on a Bruker MPA FT-NIR analyzer using the OPUS 7.0 software package. All samples were analyzed for total nitrogen using a Thermo Scientific FLASH 2000 elemental analyzer. Metabolizability, digestibility, ADF, and nitrogen content are expressed as mass percentages on ash-free dry mass basis. Period averages of these quantities, as well as vegetation height, were calculated as an average over fields weighed by the grazing pressure of each field in that period.

Excretion rate from field observations

To determine the seasonal trend in excretion rate 𝑟 (Figure 1c), we used 389 individual observations bouts, in which a single individual was followed multiple minutes, with a total duration of 96.5 h
spread out over the day and season, giving 571 dropping intervals, 27% of which were obtained on individuals carrying a GPS tracker. Interval data were fitted to a probability density function that accounted for the nonzero chance $p$ that an observer failed to see a dropping be excreted, using the methods by (Dokter et al. 2017) and associated R-package intRvals, available on CRAN (see Supplementary Material for details). Excretion observations were grouped into periods according to the midpoints between the dates of field visits.

**Energy assimilation rate $R_{\text{assim}}$**

The chemical analysis of plant and excreta can be combined with the field observations of excretion rate, to estimate the rate of energy uptake in the digestive tract: the assimilation rate $R_{\text{assim}}$. We further define the amount of body mass deposited per day as fueling rate, to be distinguished from the rate of swallowing food: the ingestion or harvest rate. The seasonal trend in the rate of energy assimilation ($R_{\text{assim}}$, Figure 2g) can be derived from the excretion rate observations in the field and the sampling program described above. The rate of energy assimilation $R_{\text{assim}}$ can be calculated as

$$R_{\text{assim}} = R_a - R_{\text{excret}} = M R_{\text{u}} = \frac{M}{(1 - M)} R_{\text{excret}} \tag{1}$$

With $R_a$ the rate of energy intake, $R_{\text{excret}}$ the rate of (excretory) energy output, and $M$ the apparent metabolizability,

$$M = 1 - \frac{[ADF]_{\text{excret}}}{[ADF]_{\text{plant}}} \frac{u_{\text{excret}}}{u_{\text{plant}}} \tag{2}$$

with $[ADF]$ the mass concentration (ash-free dry mass (AFDM) basis) of an indigestible marker (using acid detergent fiber, ADF, following Prop and Deerenberg (1991)), and $u$ the energetic content (AFDM basis). For later reference, we define apparent digestibility as $1 - [ADF]_{\text{excret}}/[ADF]_{\text{plant}}$, that is, the fraction of ingested mass (instead of ingested energy) assimilated in the body. The rate of excretory energy output equals:

$$R_{\text{excret}} = m \cdot m_{\text{excret}} \cdot u_{\text{excret}} \tag{3}$$

where $m_{\text{excret}}$ is the average ash-free dry mass of a dropping, $m$ the rate at which droppings are excreted. Filling out Equations (3) and (2) into Equation (1) gives the assimilation rate in terms of measured quantities only.

We tested $r$, $m_{\text{excret}}$, $u_{\text{excret}}$, and $M$ for seasonal trends in a linear model including terms up to third order in date, retaining the most parsimonious model as ranked by AIC, for which we report results of an $F$-test against a standard null model, $m_{\text{excret}}$, $u_{\text{excret}}$, and $M$ observations were weighed in the models by the grazing pressure factors combined, we find a seasonal increase in energy assimilation rate ($R_{\text{assim}}$, Figure 1b), combined with the energy assimilation rate $R_{\text{assim}}$ from Equation (1), as in

$$A_i = d_i \cdot R_{\text{excret}} \cdot t_i$$

$$E_i = b_i \cdot \text{BMR} \cdot t_i \tag{5}$$

with $d_i$ a binary variable (0/1) which describes whether birds were actively digesting, as inferred from location, tidal height, and accelerometer activity (see Supplementary Appendix S4). $b_i$ equals the BMR multiplier associated with a classified behavior following (Stahl 2001), and BMR the basal metabolic rate. Thermoregulatory expenditure $T_i$ was calculated according to the model by Cartar and Morrison (1997) (Baveco et al. 2011), which incorporated meteorological parameters from meteorological station “Hoorn Terschelling” (53.391205 N, 5.345746 E, WMO index number 06251, see Supplementary Figure S1), located in the study area. For daily sets of $A_i$, $E_i$, $T_i$, $P_i$, and $W_i$ values, we calculated daily sums $DA_i$, $DE_i$, $DT_i$, $DP_i$, and $DW_i$, respectively, as in $DA_i = \sum A_i$, with $i$ over all $A_i$ values of an individual within a day. Fueling trajectory modeling is described in more detail in Supplementary Appendix S4.

Modeled fueling trajectories were qualitatively compared with catch-average weights of male brent geese of all available catches in Western Europe in January–May for the period 1974–2013, as stored in the www.geese.org database. Only catches of at least 10 individual adult males are included.

**RESULTS**

**Metabolizability and harvest rate of food**

Despite an increase in grass vegetation height and standing biomass (Figure 1a), the metabolizability $M$ (Equation 2) of plant material, as calculated from the combustion energy (Figure 1b) and indigestible fiber content of grass and excreta (Figure 1c), remained constant throughout the spring season (Figure 1d, $M \sim date$, $F_{1,46} = 3.00$, $P = 0.09$). The seasonally averaged value (± standard deviation) for apparent metabolizability $M$ was 44(±9)%; apparent digestibility 39(±10)% and total nitrogen content 4.0(±0.8)%. No trend in dropping rates $r$ was observed (Figure 1e and $r \sim date$, $F_{1,27} = 2.7$, $P = 0.1$). However, the average dropping mass gradually increased during the season (Figure 1f, $m_{\text{excret}} \sim date^2 + date^3$, $F_{2,55} = 81$, $P < 0.001$), before decreasing again in the final sampling period. Geese thus gradually increased the amount of plant material processed per unit of time until shortly before departure. All factors combined, we find a seasonal increase in energy assimilation rate (Figure 1g, the product of dropping mass, dropping rate and metabolizability), related primarily to an increasing digestive throughput of food (as reflected by larger droppings).

**Time budgets**

Time budgets for all individuals are summarized for 2-weekly periods in Table 1, and trend analyses for April–May are given in Table 2. Figure 2b and Supplementary Material S3 visualizes individual time budgets. Grasslands were used for foraging almost exclusively during day time (Figure 2b). Birds roosted at night on open water or on the mudflats. We find that birds increased the daytime duration of foraging over the season (Table 1, Figure 2c).
Activity, time and energy budgets and reconstructed migratory fueling of GPS-tracked brent geese staging on agricultural grasslands of Terschelling island in spring 2013. (a) Interval at which GPS fixes were collected. (b) Habitat categories visited and accelerometer-derived activity. (c) Daily hours spent on grassland foraging area, with periods showing active body movement in green (classified as foraging) and idling periods in red (classified as digestion pauses), displayed as 1 week running averages. (d) Reconstructed components of the daily energy budget, that is, daily thermoregulatory expenditure (DT), daily existence energy (DE), and daily assimilated energy (DA), displayed as 1 week running averages. The maximum assimilation curve (green) describes the hypothetical realized daily assimilation when birds would forage continuously during daytime at a conservative assimilation rate of $R_{\text{assim}} = 120 \text{ kJ/h}$. (e) Lines: reconstructed weight changes during spring 2013 for 6 individual male brent geese. Dots: catch-average weights of male brent geese caught in Western Europe in January–May for the period 1974–1990 (black dots) and the period 1991–2013 (gray dots), as stored in the www.geese.org database. Only catches of at least 10 individual adult males are included. Colored dots indicate weights of the GPS-tagged individuals in the year of tagging (2012). Unknown body start weights in 2013 were chosen such that the fueling curves intersect the measured body weights in 2012. Panels (a)–(d) refer to individual 692.
Both the time spent on grassland, and the time spent active (including on mudflats) increased from March to May from 7.6 (0.1) to 13.3 (0.3) h. In addition, the proportion of the day spent on grasslands, and the proportion spent active, increased over time (Table 2), indicating that the time spent foraging increased more than proportional to the increase in day length. This is because in early spring (March–April), birds spent considerable time on open water, especially the first hours of the day (Figure 2b and Table 1). Birds were thus slow starters that foraged during a shorter portion of the total available daytime. As spring progressed, birds started foraging early in the day, but increasingly took short inactive bouts of less than 1 h (Figure 2b and c; Tables 1 and 2). Due to these idle bouts, the daily time spent inactive on grasslands increased.

Reconstructed energetics and fueling

We find that for all tracked individuals, the reconstructed fueling trajectories are very similar in shape (Figure 2c), and overlap, except for a difference in starting weight between individuals (Supplementary Figure S5). Productive energy became larger than zero in early April, leading to migratory fueling (i.e. when intake of energy (red line) was above the energy loss for thermoregulation (blue line), see Figure 2c). The timing of rapid mass gain and the levelling off of the fueling rate in late May were in line with independent observations of weights of caught birds (Figure 2c, black and gray dots), which also rose rapidly before reaching a plateau late May. The correspondence is best with later captures after 1990.

We may use the reconstructions of fueling trajectories to perform a sensitivity analysis of how fueling rate depended on the seasonal variation of various factors, specifically foraging duration, assimilation rate and thermoregulation (we exclude food quality, i.e. metabolizability, since it was constant throughout in our study, cf. Figure 1d). We simulated fueling trajectories under different hypothetical scenarios, using the time budget averaged over all GPS-tracked individuals. If birds would have been subject to a foraging duration different to the one of the pre-fueling period in late-May, we found that birds could potentially...
increase their body mass by at least a factor 1.37 through further extending their foraging duration (Figure 3, dark gray line), an increase that would be even larger when the period before 1 April was to be included.

**Relationship between departure weight and recruitment**

We find that during the last decade (2010–2016), only the breeding seasons of 2010, 2011, 2013, and 2014 were successful, as indicated by a high percentage of juveniles in captures in the subsequent spring (22% (n = 127), 33% (n = 133), 52% (n = 67), 46% (n = 70), respectively, see Supplementary Table S2). In other years, the percentage of juveniles was below 5%, likely because of poor breeding conditions associated to the lemming cycle in the Arctic (Nolet et al. 2013). In total, 95 adult females and 111 adult males were marked and weighed at the study site in springs with successful reproduction, indicating a significant male sex bias (z = −5.4, n = 206, 2-sided P < 0.001). These 206 individuals were used for further analyses. At the study site, 86% of the females and 94% of the males returned, as determined from 3444 individual resightings in the autumn or spring directly following the year of capture, amounting to an average of 18 resightings per marked individual per season. For 53% of resighted adults, the family size was noted, which ranged from 1 to 5 juveniles, on average 2.5 (±1.2).

Based on these mark-resightings, the relation between adult departure weight and recruitment success was quantified (Figure 4), following Ebbinge and Spaans (1995). Adults returning to the study site with offspring had higher than average departure weights in the preceding spring, both in the case of fathers (Mann–Whitney U = 1571, n₁ = 108, n₂ = 37, P < 0.05) and mothers (Mann–Whitney U = 1271, n₁ = 93, n₂ = 46, P < 0.001), indicating that adults with higher body stores produced more offspring. The differences in body weight distribution (Figure 4) were significant for the structural mass index [SMI] (2-sample Kolmogorov–Smirnov test, males: n₁ = 108, n₂ = 37, P = 0.03, females: n₁ = 93, n₂ = 46, P = 0.002), as well for uncorrected body mass (males P = 0.005, females P = 0.0001).

**DISCUSSION**

We studied brent geese preparing for migration in spring and expected brent geese fueling on agricultural pasture to frequently loaf and rest, and no longer show a relationship with departure weight and reproductive success. We will discuss these 2 expectations in the following sections.

Are geese fueling in the midst of plenty on fertilized pastures?

If pasture grassland provides a regime of food abundance, we predicted birds to loaf and frequently be inactive, as an indication that birds do not experience strong time constraints. We find...
indeed that—especially in the earlier stages of spring—geese did not fuel as much as they could, using a smaller proportion of the day for foraging in early spring than in later spring. During the hyperphagic peak fueling period in May, birds were further observed to be increasingly inactive for short periods of time. These resting boutts were shorter than the average retention time (Prop and Vulink 1992), which we therefore considered to be digestion bouts. Food availability became so high that ingestion rates likely increased, and birds rapidly met their digestive bottleneck (Kersten and Visser 1996).

The observations of brent geese not requiring the full daytime for foraging in early spring, and the frequent digestion bouts in later spring, both suggest that birds were fueling in an environment where food was indeed abundant, such that harvesting food required a relatively limited amount of time. The periods of inactivity suggest that time-constraints on the harvesting process of food were no longer present. In early spring, the inactive time amounts to feeding time, which in case of need can be used to harvest more food and increase the daily assimilated energy. In later spring, the inactive time refers to digestion pauses. This idle time cannot be used for additional energy assimilation, but it does lift time constraints on the harvest and grazing process for individuals that have lower harvest rates (i.e. they would simply have fewer digestive pauses).

Besides a high abundance, grass quality was also of high quality and remained so throughout the season (Figure 1d). Birds likely succeeded in keeping grass in a short high-quality state by repeatedly grazing the same fields, especially by aggregating on the fields close to the intertidal (data not shown) (Bos et al. 2004). Birds were left undisturbed by humans, as our study site was managed as a refuge for geese and meadow birds (neither any predator attacks were observed). This management provided conditions in which birds could freely revisit sites and keep up with the high growth rate of fertilized grassland.

The values for the digestibility and nitrogen content of grass found in this study are among the highest reported for graminoids grazed by brent geese (Bouwmeijer 1994; Hassall et al. 2001), and therefore can be considered a relatively high-quality resource for fueling.

Grass quality, thus, did not explain any changes in fueling rates at our study site. In fact, the sensitivity analysis of our fueling trajectories suggests that brent geese achieved fueling primarily by simply eating for a longer proportion of the day, followed by increasing their harvest rate and digestive throughput. Compared with these effects, release from thermoregulatory costs was of limited importance at our site.

Our pastures are a monoculture with little heterogeneity (see Supplementary Figure S4), where the high food availability shortens harvesting time. Released from time constraints, we expect that effects related to competitive ability of geese are here of less importance than in heterogeneous habitats, because sub-ordinate birds are expected to have sufficient time to compensate for a lower harvest rate, and become digestion-rate limited too. We indeed found that the interaction rate at our study site to be up to 3–4 times lower than at a nearby saltmarsh (Dokter et al. 2018b, Supplementary Figure S6). This contrasts with the common notion that flock-feeding geese are in strong competition for the best food plants (Mclandress and Raveling 1981; Gauthier et al. 1984; Teunissen et al. 1985; Prop and Deerenberg 1991; Black et al. 1992; Stahl et al. 2001; Bos et al. 2005). These studies were performed in heterogeneous natural staging habitats, like saltmarshes, or in areas where birds compete for patchy waste crop, where competitive interactions over food are much more likely to become effective.

An apparent paradox: why do body stores still correlate with fitness?

Our analysis of recruitment in relation to departure body stores does not support our initial prediction that birds fueling amidst abundant high-quality food would all reach sufficient departure stores. We find a persisting correlation between recruitment and departure weight, corroborating results found 3 decades ago for dark-bellied brent geese on a combination of saltmarsh habitat, extensively grazed saltmarsh, and agricultural pasture (Ebbinge 1989; Ebbinge and Spans 1993). Apparently, this relation persists, even when restricting analyses to brent geese fueling on the recent homogenous monoculture with a constant high food availability.

This result leads to an apparent paradox: why do we observe substantial differences in departure weights that are strongly correlated with fitness (Figure 4), whereas the foraging conditions on agricultural grasslands provide sufficient leeway to accumulate extra body stores? We hypothesize that leaner birds were incapable of acquiring more stores, not as a result of limited access to food, but as a product of a bird’s internal vitality, digestive system, health status, parasite load, immuno-competence, and other inherent quality differences between individuals, which may be determined by longer-term individual life history. Such quality differences could also be related to age and pair bond duration (Black 2001), (density-dependent) factors experienced during early life (Fay et al. 2017), as well as social status (Wilson and Nussey 2010; Klaassen et al. 2012; Clausen et al. 2015). The peak hyperphagic period (May), when birds are likely limited by digestion and day length, may be considered the most critical period during pre-migratory staging. Poor health or other factors that reduce the digestive capacity in this period can no longer be compensated in a later stage and affect most directly the final body stores. Also, the physiological flexibility to increase digestion efficiency and capacity will be important (Hume and Biebach 1996; Piersma and Lindström 1997). Interestingly, our reconstructions of fueling trajectories were highly similar for different individuals, because birds did not differ substantially in their high-resolution time budgets (Supplementary Figure S5). However, we should note that these simulations did not take into account individual differences in internal parameters, like the cost of mass change χ or digestive capacity. Differences in final fuel loads may well be driven by such physiology-, digestion-, and health-related factors, instead of by differences in time budgets and accessibility to food. Our study calls for experimental manipulations of individuals to unravel the flexibilities in the timing and duration of hyperphagy, the efficiency of the digestive machinery and its response to pathogen challenges, whose associated trade-offs cannot be studied with observational data alone.

In recent decades, food limitations during the pre-migratory period in spring have likely been lifted for arctic-breeding waterfowl by agricultural intensification (Abraham et al. 2003), in the case of grassland by artificial improvements by fertilizers (Spans and Postma 2001; Van Eerden et al. 2005; Eichhorn et al. 2012). Fitness correlations with departure weight have nonetheless persisted in our study system, suggesting that aspects of individual quality like internal vitality may be important in determining final fuel stores. These factors can be related to life histories over longer time periods than the fueling period alone, which calls for studies integrating across life-history stages. In the case of brent geese, consideration of the autumn and winter staging period on selgrass beds may be important (Inger et al. 2010).
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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Dokter et al. (2018a).

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