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

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

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## **Title**

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

## **Abstract**

Long-distance migratory birds rely on 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 fuelling site. Here we studied how food abundance during fuelling 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) that birds would reach sufficient fuel loads, such that departure weight would no longer affect reproductive success. Our study system comprised brent geese (*Branta b. bernicla*) staging on high-quality agricultural pastures. Fuelling conditions were assessed by a combination of high-resolution GPS-tracking, acceleration-based behavioural classification, thermoregulation modelling, 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 fuelling in early spring, and took frequent digestion pauses, suggesting that traditional time constraints on harvest and fuelling 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 fuelling period.

### **Key-words**

arctic waterfowl, cultivated grassland, recruitment, GPS tracking, migratory fuelling  
carry-over effects

## **Introduction**

Long-distance migration is a highly athletic period in the annual cycle of migratory animals. In order to migrate and breed successfully, migrants need to build sufficient body stores and muscle capacity before departure (Prop et al. 2003; Inger et al. 2008). Many studies have suggested the existence of carry-over effects of the pre-migratory fuelling stage into the breeding stage (Studds and Marra 2005; Inger et al. 2010; Sedinger et al. 2011; Legagneux et al. 2012; Harrison et al. 2013). Failing to secure sufficient stores prior to migration and breeding may have negative impacts on breeding success (Drent et al. 2003; Legagneux et al. 2012), which highlights the importance of fuelling periods.

The fuel loads acquired by migrants are thought to strongly depend on the availability and quality of food at pre-migratory staging sites (Metcalf and Furness 1984; Prop and Deerenberg 1991; Lindström 2002). Geese and shorebirds have even been referred to as 'prisoners of their food supply' during pre-migratory 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. 1985; Prop and Deerenberg 1991; Black et al. 1992; Inger et al. 2010).

Fuelling 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 fuelling 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. 2016). Fuelling on man-made habitats also includes pastures for ducks (Owen and Williams 1976) and plovers (Gillings et al. 2007), orchards for songbirds (Rey 2011), and rice and corn fields for waders and waterbirds (McLandsress and Raveling 1981; Guzmán 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 to 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 fuelling 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 fuelling-related carry-over effects of departure condition into the breeding season will be absent.

We studied these issues in dark-bellied brent geese (*Branta b. 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 fuelling 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). Fuelling in spring occurs predominantly on agricultural grasslands. During fuelling geese occupy only a limited area of available grasslands, which they graze repeatedly to keep the grass in a young nutritious state (Bos, Van De Koppel, and Franz J. Weissing 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 fuelling simulations that reconstructed the birds' fuelling trajectories, which were used to rank factors affecting the birds' mass increase through a sensitivity analysis.

If constraints associated with food on spring fuelling 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 colour 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 km<sup>2</sup> contiguous agricultural grasslands, which are managed as a goose fuelling 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 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 minutes 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 supporting information). 11 birds were contacted at the catching site after the breeding season, of which seven birds returned for migratory fuelling 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 behaviour (verified with camera observations of GPS-tagged captive birds, see

supplemental); within active behaviour, flying, with its characteristically high acceleration variation (Shamoun-Baranes et al. 2012), was scored separately. Combining accelerometer activity (see Table S1 and 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, 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 analysed using a linear mixed model for each time budget category, using the lme function of R-package nlme (Pinheiro et al. 2017). We considered date as fixed effect, and individual as random intercept effect, as in  $\text{activity} \sim \text{date} + (1|\text{ID})$ . 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 2010-2016, i.e. 1-2 weeks before departure at the end of May, with each year having 1-2 catches within 3 days (see Table S2). Individuals were colour-ringed with unique codes, and weighed within a few hours after capture. The study site was visited almost daily by field observers from October-May, who noted down colour 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 (SMI, see supplementary appendix S3), using standardised 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 organised in multiple transects of increasing distance to the intertidal (see supplementary Fig. S1), such that fields exposed to different grazing intensities were included in the programme. On each field, a 1 m<sup>2</sup> enclosure was put in place on 13 March 2013, which was moved by several metres into a new position during field visits every two weeks. Plant material was collected from inside the enclosure on Mar 26, April 10, April 21, May 8 and May 21. During each field visit, we quantified grazing pressure per field (in droppings/m<sup>2</sup>) by counting droppings in five circles of 4 m<sup>2</sup>, which were cleared each visit and of which the centres were marked by inconspicuous 5 cm protruding sticks. From each circle, two droppings were collected as fresh as possible. To measure vegetation height in each circle and inside the enclosure, 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 analysed for acid detergent fibre (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-infrared reflectance

spectroscopy on a Bruker MPA FT-NIR analyser using the OPUS 7.0 software package. All samples were analysed for total nitrogen using a Thermo Scientific FLASH 2000 elemental analyzer. Metabolisability, 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  $r$  (Fig. 1e), we used 389 individual observations bouts, in which a single individual was followed multiple minutes, with a total duration of 96.5 hours spread out over the day and season, giving 571 dropping intervals, 27% of which were obtained on individuals carrying a GPS tracker. Interval data was 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 supporting information for details). Excretion observations were grouped into periods according to the midpoints between the dates of field visits.

### ***Energy assimilation rate $R_{assim}$***

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*  $R_{assim}$ . We further define the amount of body mass deposited per day as *fuelling rate*, to be distinguished from the rate of swallowing food: the *ingestion or harvest rate*. The seasonal trend in the rate of energy assimilation ( $R_{assim}$ , Fig. 2g) can

be derived from the excretion rate observations in the field and the sampling programme described above. The rate of energy assimilation  $R_{assim}$  can be calculated as

$$R_{assim} = R_{in} - R_{out} = MR_{in} = \frac{M}{(1 - M)} R_{out} \quad (1)$$

With  $R_{in}$  the rate of energy intake,  $R_{out}$  the rate of (excretory) energy output, and  $M$  the apparent metabolisability,

$$M = 1 - \frac{[ADF]_{grass}}{[ADF]_{excreta}} \cdot \frac{u_{excreta}}{u_{grass}} \quad (2)$$

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

$$R_{out} = r \cdot m_{excreta} \cdot u_{excreta} \quad (3)$$

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

We tested  $r$ ,  $m_{excreta}$ ,  $u_{excreta}$ , 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 an results of an F-test against a standard null model.  $m_{excreta}$ ,  $u_{excreta}$ , and  $M$  observations were weighed in the models by the grazing pressure of the field where material was collected. The trend in  $R_{assim}$  was obtained by combining quantities according to Eq. (1)-(3), retaining only the significant date model terms.

## Integrating data to reconstruct energy balance and fuelling

For each time interval  $i$  of duration  $t_i$  (corresponding to one GPS fix), we calculated productive energy  $P_i$  as the energy assimilated above the amount needed for existence  $E_i$  and thermoregulation  $T_i$  (Paladino and King 1984; Blaxter 1989):

$$\begin{aligned} P_i &= A_i - \max[E_i, T_i] \\ W_i &= P_i/\gamma \end{aligned} \quad (4)$$

with  $W_i$  the bird's change in body stores assuming a cost of mass change  $\gamma$  (kJ/g).

Assimilated energy ( $A_i$ ) and existence energy ( $E_i$ ) were derived from time budgets calculated from an accelerometer-based behavioural classification (Table S1), combined with the energy assimilation rate  $R_{assim}$  from Eq. (1), as in

$$\begin{aligned} A_i &= d_i \cdot R_{assim} \cdot t_i \\ E_i &= b_i \cdot BMR \cdot t_i \end{aligned} \quad (5)$$

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 appendix S4).  $b_i$  equals the BMR multiplier associated with a classified behaviour following (Stahl 2001), and BMR the basal metabolic rate. Thermoregulatory expenditure  $T_i$  was calculated according to the model by Cartar & 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 Fig. 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  $DA$ ,  $DE$ ,  $DT$ ,  $DP$  and  $DW$ , respectively, as in  $DA = \sum_i A_i$ , with  $i$  over all  $A_i$  values of an individual within a day. Fuelling trajectory modelling is described in more detail in supplementary material Appendix S4.

Modelled fuelling trajectories were qualitatively compared to 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](http://www.geese.org) database. Only catches of at least 10 individual adult males are included.

## Results

### *Metabolisability and harvest rate of food*

Despite an increase in grass vegetation height and standing biomass (Fig. 1a), the metabolisability  $M$  (Eq. 2) of plant material, as calculated from the combustion energy (Fig. 1b) and indigestible fibre content of grass and excreta (Fig. 1c), remained constant throughout the spring season (Fig. 1d,  $M \sim \text{date}$ ,  $F_{114}=3.00$ ,  $p=0.09$ ). The seasonally averaged value ( $\pm$  standard deviation) for apparent metabolisability  $M$  was 44 ( $\pm 9$ ) %, apparent digestibility 39 ( $\pm 10$ ) % and total nitrogen content 4.0 ( $\pm 0.8$ ) %. No trend in dropping rates  $r$  was observed (Fig. 1e,  $r \sim \text{date}$ ,  $F_{566}=2.7$ ,  $p=0.1$ ). However, the average dropping mass gradually increased during the season (Fig. 1f,  $m_{\text{excreta}} \sim \text{date}^2 + \text{date}^3$ ,  $F_{25}=81$ ,  $p<0.001$ ), 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 (Fig. 1g, the product of dropping mass, dropping rate and metabolisability), related primarily to an increasing digestive throughput of food (as reflected by larger droppings).

### *Time budgets*

Time budgets for all individuals are summarized for two-weekly periods in Table 1, and trend analyses for Apr-May are given in Table 2. Fig. 2b and S3 visualizes individual time budgets. Grasslands were used for foraging almost exclusively during day time (Fig. 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, Fig. 2c).

Both the time spent on grassland, and the time spent active (including on mudflats) increased from Mar-May from 7.6 (0.1) to 13.3 (0.3) hours. 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 (Mar-Apr), birds spent considerable time on open water, especially the first hours of the day (Fig. 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 one hour (Fig. 2b/c, Table 1,2). Due to these idle bouts, the daily time spent inactive on grasslands increased.

#### *Reconstructed energetics and fuelling*

We find that for all tracked individuals, the reconstructed fuelling trajectories are very similar in shape (Fig. 2e), and overlap apart from the difference in starting weight between individuals (Fig. S5). Productive energy became larger than zero in early April, leading to migratory fuelling (i.e. when intake of energy (red line) was above the energy loss for thermoregulation (blue line), see Fig. 2e). The timing of rapid mass gain and the levelling off of the fuelling rate in late May were in line with independent observations of weights of caught birds (Fig. 2e, 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 fuelling trajectories to perform a sensitivity analysis of how fuelling rate depended on the seasonal variation of various factors, specifically foraging duration, assimilation rate and thermoregulation (we exclude food quality, i.e. metabolisability, since it was constant throughout in our study, cf. Fig. 1d).

We simulated fuelling trajectories under different hypothetical scenarios, in which the seasonal variation in one of these factors was removed, while leaving all other factors unmodified as measured. Figure 3 illustrates the outcome of different hypothetical scenarios, using the time budget averaged over all GPS-tracked individuals. If birds would have been subject to a foraging duration (Fig. 3, black), assimilation rate (Fig. 3, light grey) or thermoregulation cost (Fig. 3, dashed) of the pre-fuelling period in late-March, when conditions are likely harsher than in later periods, they would have reached a final body mass reduced by a factor 0.50, 0.68 or 0.88, respectively. During peak fuelling in early May, time budgets reveal that birds spent at most two daytime hours not actively digesting. By extrapolating this time budget to the entire fuelling period (Apr-May), we found that birds could potentially increase their body mass by at least a factor 1.37 through further extending their foraging duration (Fig. 3, dark gray line), an increase that would be even larger when the period before April 1 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 the subsequent spring (22% (n=127), 33% (n=133), 52% (n=67), 46% (n=70), respectively, see 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 ( $z=-5.4$ ,  $n=206$ , two-sided  $p<0.001$ ). These 206 individuals were used for further analyses. 86% of the females and 94% of the males returned at

the study site, 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 1-5 juveniles, on average 2.5 ( $\pm 1.2$ ). Based on these mark-resightings, the relation between adult departure weight and recruitment success was quantified (Fig. 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  $U=1571$ ,  $n_1=108$ ,  $n_2=37$ ,  $p<0.05$ ) and mothers (Mann-Whitney  $U=1271$ ,  $n_1=93$ ,  $n_2=46$ ,  $p<0.001$ ), indicating that adults with higher body stores produced more offspring. The differences in body weight distribution (Fig. 4) were significant for the structural mass index (SMI) (two-sample Kolmogorov-Smirnov test, males:  $n_1=108$ ,  $n_2=37$ ,  $p=0.03$ , females:  $n_1=93$ ,  $n_2=46$ ,  $p=0.002$ ), 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 two expectations in the following sections.

### *Are geese fuelling 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 fuelling period in May, birds were further observed to be increasingly inactive for short periods of time. These resting bouts 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 fuelling 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 loafing 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 (Fig. 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, Van De Koppel, and Franz J Weissing 2004). Birds were left undisturbed by humans, since 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 higher reported for graminoids grazed by brent geese (Boudewijn 1984; Hassall et al. 2001), and therefore can be considered a relatively high quality resource for fuelling.

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

Our pastures are a monoculture with little heterogeneity (see Fig. S4), where the high food availability makes harvesting take little 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 (in review, relevant figure included in supplemental Fig. S6). This contrasts with the common notion that flock-feeding geese are in strong competition for the best food plants (McLandsress 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 fuelling 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 Spaans 1995). Apparently, this relation persists, even when restricting analyses to brent geese fuelling on the recent homogenous monoculture with a constant high food availability.

This results leads to an apparent paradox: why do we observe substantial differences in departure weights that are strongly correlated with fitness (Fig. 4), while the foraging conditions on agricultural grasslands provide sufficient leeway to accumulate extra body stores? We hypothesise 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, immunocompetence, 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 impact 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 fuelling

trajectories were highly similar for different individuals, because birds did not differ substantially in their high-resolution time budgets (Fig. S5). However, we should note that these simulations did not take into account individual differences in internal parameters, like the cost of mass change  $\gamma$  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 hyperphagia, 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. 2005), in the case of grassland by artificial improvements by fertilizers (Spaans 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 fuelling 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 eelgrass beds may be important (Inger et al. 2010).

## **Data Accessibility**

Data will be stored on Dryad.

## **Acknowledgements**

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## Figure Legends

Figure 1: Reconstruction of the seasonal trend in energy assimilation rate  $R_{assim}$  from chemical analyses of plant and excreta material and dropping rate observations. (a) Mean and standard deviation of vegetation height on the sampled fields (grey, n=27 fields) and on the grazed fields (black dots). (b) Ash-free dry mass energy content of grass and excreta. (c) Acid detergent fibre (ADF) content of grass and excreta. (d) Apparent metabolisability of the plant material (e) Dropping rates derived from field observations (f) Mean and standard deviation of the ash-free dropping mass. (g) final result of the assimilation rate  $R_{assim}$ , from combining all sub-trends according to equations 1 and 2. Dashed lines are significant linear model trends including date-effects up to third order.

Figure 2: Activity, time and energy budgets and reconstructed migratory fuelling 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, i.e. 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 realised daily assimilation when birds would forage continuously during daytime at a conservative assimilation rate of  $R_{assim}=120$  kJ/h. (e) Lines: reconstructed weight changes during spring 2013 for six 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 1990-2013 (grey dots), as stored in the [www.geese.org](http://www.geese.org) database. Only catches of at least 10 individual adult males are included. Coloured 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 fuelling curves intersect the measured body weights in 2012. Panels (a)-(d) refer to individual 692.

Figure 3: Simulated fuelling trajectories under four hypothetical scenarios, and the reference equal to the average of the trajectories of Fig 2e (thick line). (1) black: constant foraging duration of 8.7 h/day, the value observed before hyperphagia (second half of March). (2) dark grey: foraging duration equalling daytime minus 1.9 hours, the average time not spent foraging during the first half of May. (3) light grey: constant assimilation rate of  $R_{assim}=118$  kJ/h, the value observed before hyperphagia. (4) dashed: constant thermoregulation costs as the mean value observed value before hyperphagia (955 kJ/day). Fuelling results primarily from an increase in foraging duration, which realises a factor 0.5 of the total mass gain, whereas increase in assimilation rate realises a factor  $1-0.68=0.32$ . There was a substantial time surplus available to extend the foraging duration in April, by which the mass gain could potentially be increased by a factor 1.37.

Figure 4: Histograms of the pre-migratory departure weight of all marked adults (light grey) and of parents with juveniles in the juvenile's year of birth (dark grey), according to adult sex (top: males, bottom: females). Parent weight was included once for each juvenile family member. The departure weight of adults with juveniles is significantly

biased towards higher departure weights (dark grey), relative to the average distribution of adult male and female departure weight (light grey), suggesting adult brent with higher pre-migratory body stores returned with more offspring from the breeding grounds. Histograms are shown for measured weights uncorrected for structural size.

## Tables and table legends

Table 1: Seasonal activity budgets during daytime

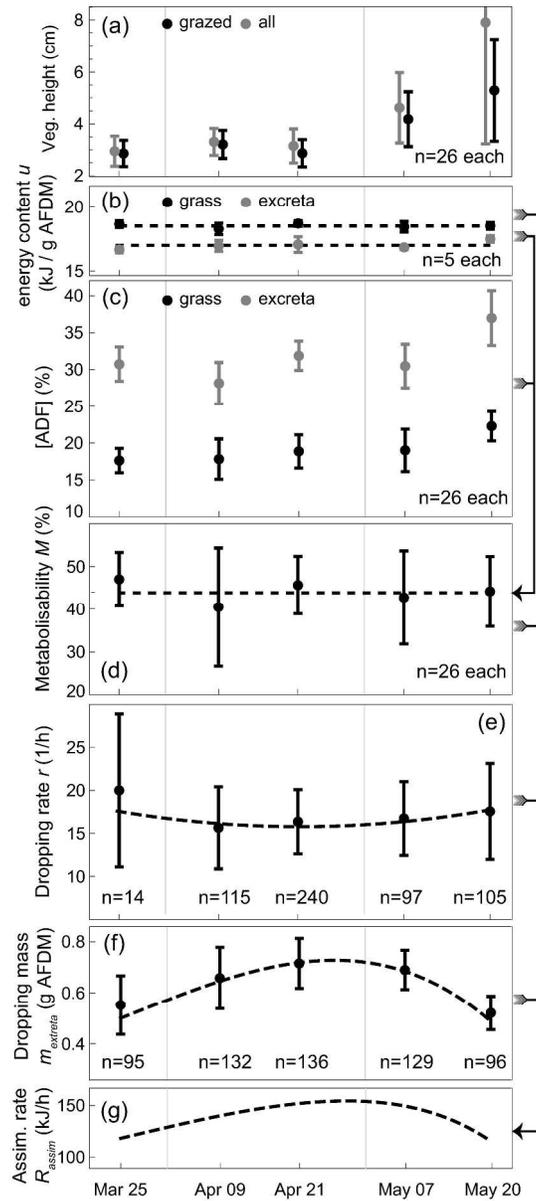
period	birds	on pasture (h)	active (h)	rest (h)	flight (h)	On pasture (0-1)
1 Jan-II	3	9.1 (0.4) <sup>a</sup>	8.6 (0.5) <sup>a</sup>	0.5 (0.1) <sup>a</sup>	0.5 (0.1) <sup>a</sup>	1.00 (0.08)
2 Feb-I	3	7.6 (0.1) <sup>b</sup>	7.4 (0.1) <sup>b</sup>	0.2 (0.1) <sup>b</sup>	0.4 (0.1) <sup>a</sup>	0.81 (0.01) <sup>a,b,e</sup>
3 Feb-II	3	7.6 (0.3) <sup>b</sup>	7.3 (0.3) <sup>b</sup>	0.2 (0.1) <sup>b</sup>	0.5 (0.2) <sup>a</sup>	0.73 (0.03) <sup>c</sup>
4 Mar-I	3	8.2 (0.5) <sup>b</sup>	7.8 (0.5) <sup>b,c</sup>	0.4 (0.2) <sup>a</sup>	0.5 (0.3) <sup>a</sup>	0.72 (0.05) <sup>b,c</sup>
5 Mar-II	3	9.5 (0.1) <sup>a</sup>	9.0 (0.4) <sup>a,c,d</sup>	0.4 (0.2) <sup>a</sup>	0.8 (0.2) <sup>a</sup>	0.76 (0.01) <sup>c</sup>
6 Apr-I	6	9.8 (0.5) <sup>a</sup>	9.3 (0.8) <sup>a,d</sup>	0.5 (0.3) <sup>a</sup>	0.6 (0.2) <sup>a</sup>	0.72 (0.04) <sup>c</sup>
7 Apr-II	6	10.9 (0.3) <sup>c</sup>	9.3 (0.5) <sup>a,d</sup>	1.6 (0.6) <sup>c</sup>	0.6 (0.1) <sup>a</sup>	0.75 (0.02) <sup>c</sup>
8 May-I	6	13.3 (0.5) <sup>d</sup>	10.5 (0.7) <sup>e</sup>	2.8 (1.1) <sup>c,d</sup>	0.5 (0.1) <sup>a</sup>	0.86 (0.03) <sup>d</sup>
9 May-II	4	13.3 (0.5) <sup>d</sup>	10.0 (0.6) <sup>d,e</sup>	3.3 (0.3) <sup>d</sup>	0.4 (0.1) <sup>a</sup>	0.82 (0.03) <sup>d,e</sup>

Daily hours spent on pastures, active, resting and in flight averaged over individuals by two-weekly period, mean (standard deviation). Last column gives proportion of total daytime spent on grassland. Values within the same column with non-corresponding superscript characters are significantly different on a  $\alpha=0.05$  significance level according to a Mann-Whitney U test, after Benjamini-Hochberg correction for multiple comparisons within columns (n=36 pairs).

Table 2:

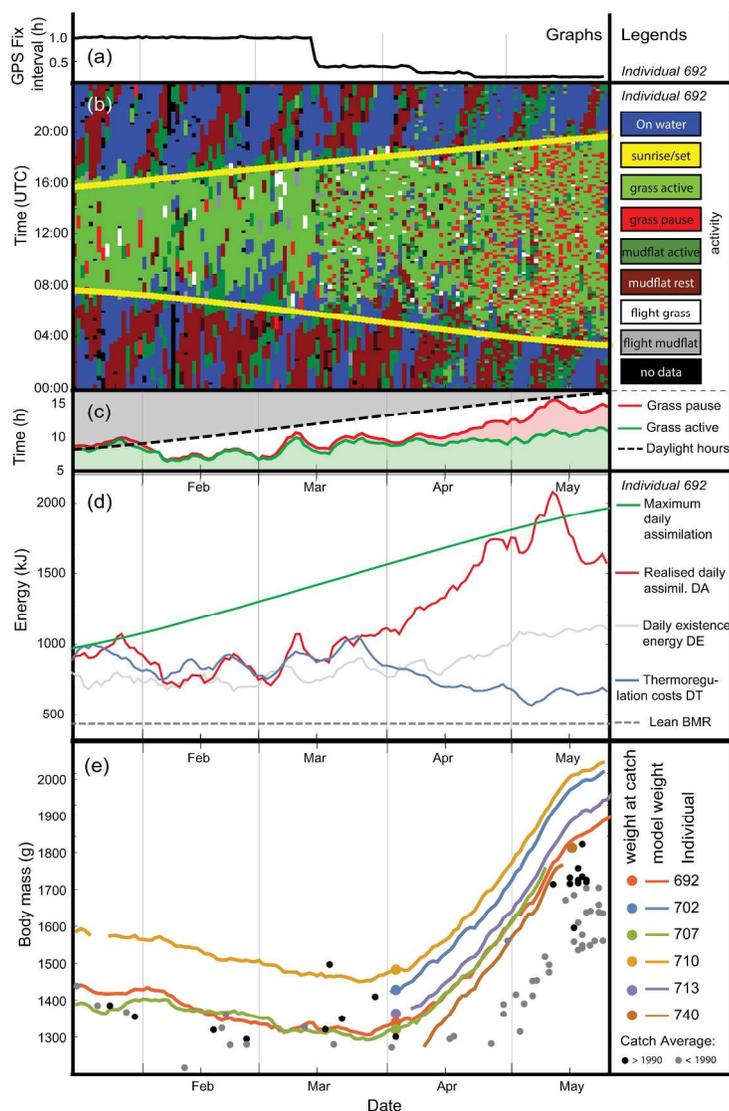
Activity		Model analysis		
		Intercept	Day	p
Day	<b>Pasture active</b>	0.59 (0.02) ***	0.0009 (0.0003) *	0.014
Day	<b>Pasture rest</b>	0.01 (0.02)	0.0042 (0.0003) ***	<0.0001
Day	<b>On water</b>	0.130 (0.007) ***	-0.0023 (0.0002) ***	<0.0001
Day	<b>Mudf. active</b>	0.125 (0.006) ***	-0.0012 (0.0002) ***	<0.0001
Day	<b>Mudflat rest</b>	0.096 (0.007) ***	-0.0011 (0.0002) ***	<0.0001
Day	<b>Fly</b>	0.047 (0.003) ***	-0.0005 (0.0001) ***	0.001
Night	Pasture active	0.019 (0.004) ***	-0.0001 (0.0001)	0.5
Night	Pasture rest	0.004 (0.002)	0.00004 (0.00007)	0.5
Night	On water	0.45 (0.02) ***	-0.0008 (0.006)	0.2
Night	Mudf. active	0.23 (0.02) ***	-0.0004 (0.0004)	0.3
Night	Mudflat rest	0.29 (0.03) ***	0.0011 (0.0006)	0.06
Night	Fly	0.007 (0.002) *	0.00011 (0.00007)	0.08

Trend analysis of individual Brent Goose activities for the months Apr-May, expressed as the daily proportion of time spent in each activity category. Activity categories with a significant seasonal trend in a mixed model analysis are highlighted in **bold**. Fixed effect estimates (and standard error) were estimated by REML. Significance of model terms are indicated in stars (\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ) according to a t-test. p gives the p-value of a likelihood ratio test against a constant null model. Parameter Day equals days since Apr 1. Over the season, geese spent proportionally more time on pastures being active and resting, and less time on water, mudflats or flying during daytime. No nighttime trends were found.

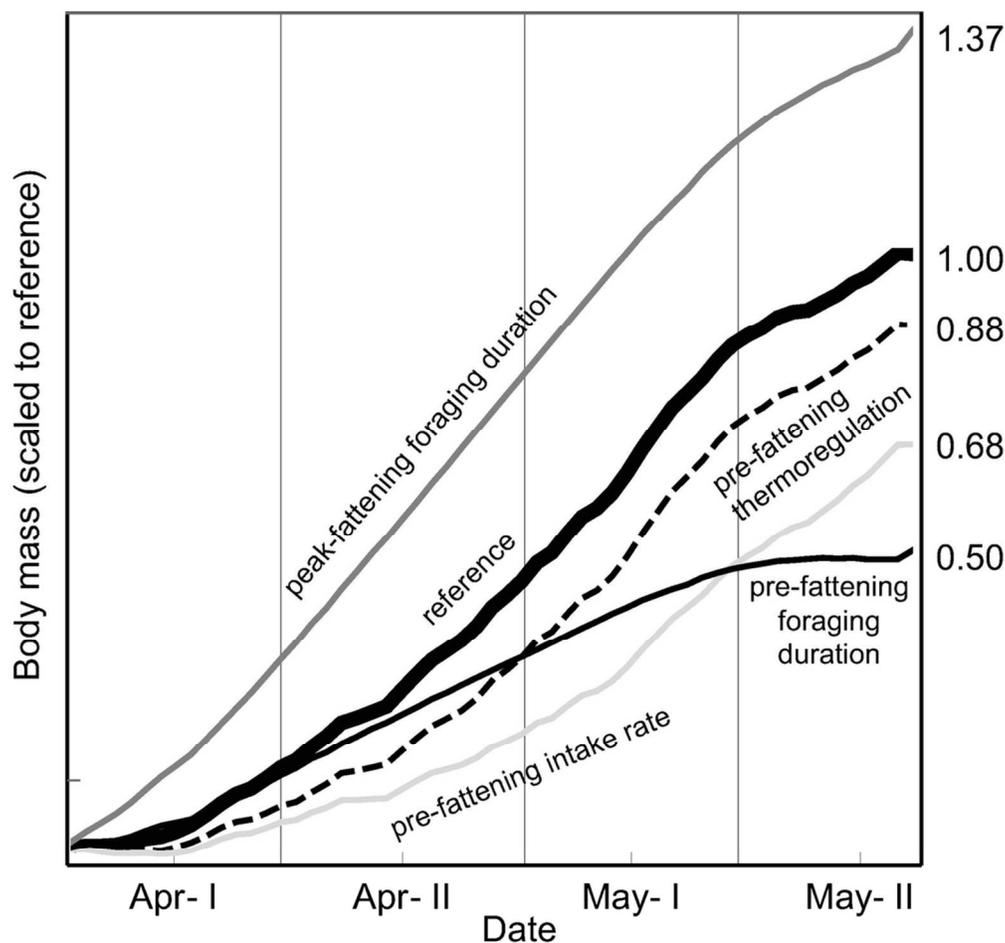


Reconstruction of the seasonal trend in energy assimilation rate  $R_{assim}$  from chemical analyses of plant and excreta material and dropping rate observations. (a) Mean and standard deviation of vegetation height on the sampled fields (grey,  $n=27$  fields) and on the grazed fields (black dots). (b) Ash-free dry mass energy content of grass and excreta. (c) Acid detergent fibre (ADF) content of grass and excreta. (d) Apparent metabolisability of the plant material (e) Dropping rates derived from field observations (f) Mean and standard deviation of the ash-free dropping mass. (g) final result of the assimilation rate  $R_{assim}$ , from combining all sub-trends according to equations 1 and 2. Dashed lines are significant linear model trends including date-effects up to third order.

220x493mm (300 x 300 DPI)

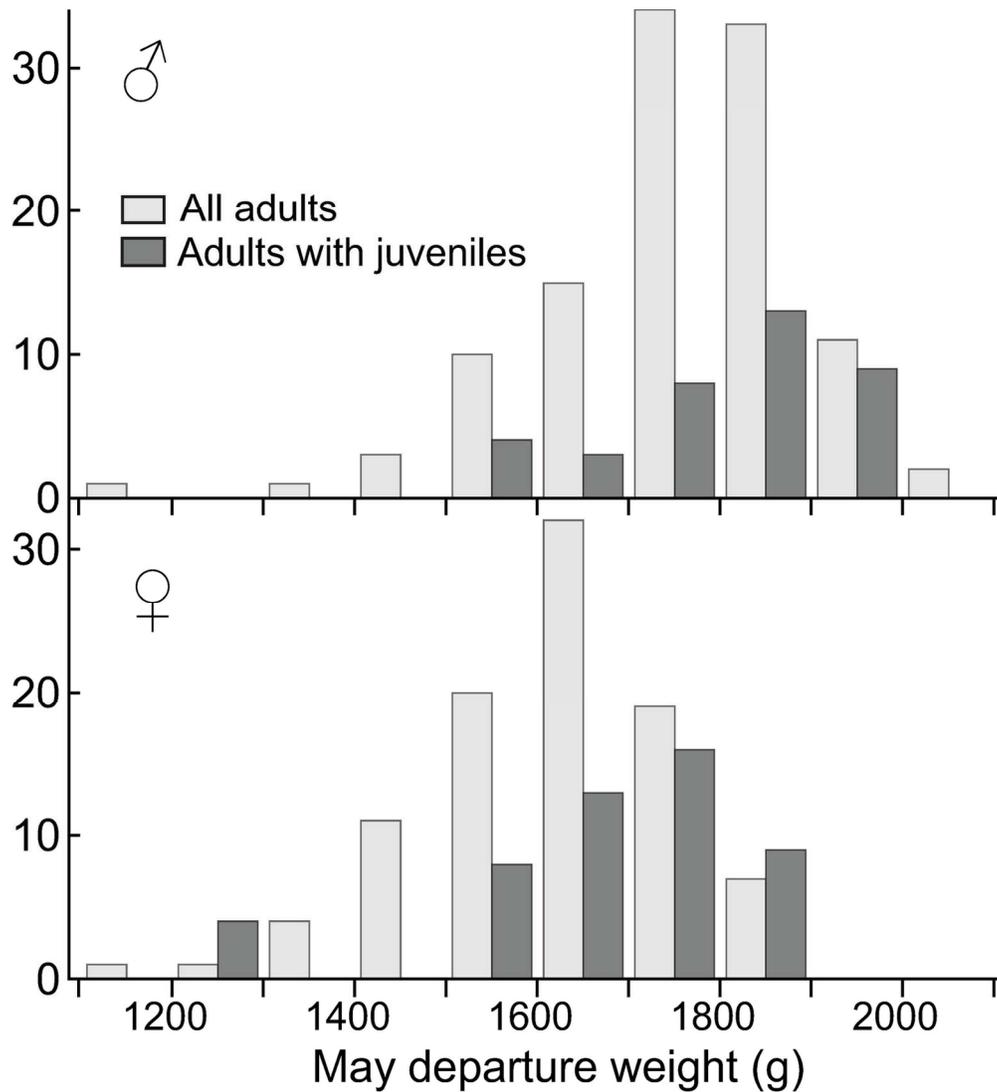


Activity, time and energy budgets and reconstructed migratory fuelling of GPS-tracked brent geese staging on agricultural grasslands of Terschelling island in spring 2013. (a) Interval at which GPS fixes were collected (b) habitat categories visited and accelerometer-derived activity (c) Daily hours 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, i.e. 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 realised daily assimilation when birds would forage continuously during daytime at a conservative assimilation rate of  $R_{assim}=120$  kJ/h. (e) Lines: reconstructed weight changes during spring 2013 for six 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 1990-2013 (grey dots), as stored in the [www.geese.org](http://www.geese.org) database. Only catches of at least 10 individual adult males are included. Coloured dots indicate weights of the GPS-tagged individuals in the year of tagging (2012). Unknown body start weights in 2012 were chosen such that the fuelling curves intersect the measured body weights in 2012. Panels (a)-(d) refer to individual 692.



Simulated fuelling trajectories under four hypothetical scenarios, and the reference equal to the average of the trajectories of Fig 2e (thick line). (1) black: constant foraging duration of 8.7 h/day, the value observed before hyperphagia (second half of March). (2) dark grey: foraging duration equalling daytime minus 1.9 hours, the average time not spent foraging during the first half of May. (3) light grey: constant assimilation rate of  $R_{assim}=118$  kJ/h, the value observed before hyperphagia. (4) dashed: constant thermoregulation costs as the mean value observed value before hyperphagia (955 kJ/day). Fuelling results primarily from an increase in foraging duration, which realises a factor 0.5 of the total mass gain, whereas increase in assimilation rate realises a factor  $1-0.68=0.32$ . There was a substantial time surplus available to extend the foraging duration in April, by which the mass gain could potentially be increased by a factor 1.37.

93x88mm (300 x 300 DPI)



Histograms of the pre-migratory departure weight of all marked adults (light grey) and of parents with juveniles in the juvenile's year of birth (dark grey), according to adult sex (top: males, bottom: females). Parent weight was included once for each juvenile family member. The departure weight of adults with juveniles is significantly biased towards higher departure weights (dark grey), relative to the average distribution of adult male and female departure weight (light grey), suggesting adult brent with higher pre-migratory body reserves returned with more offspring from the breeding grounds. Histograms are shown for measured weights uncorrected for structural size.

138x151mm (300 x 300 DPI)

## Supplementary Data

Figure S1

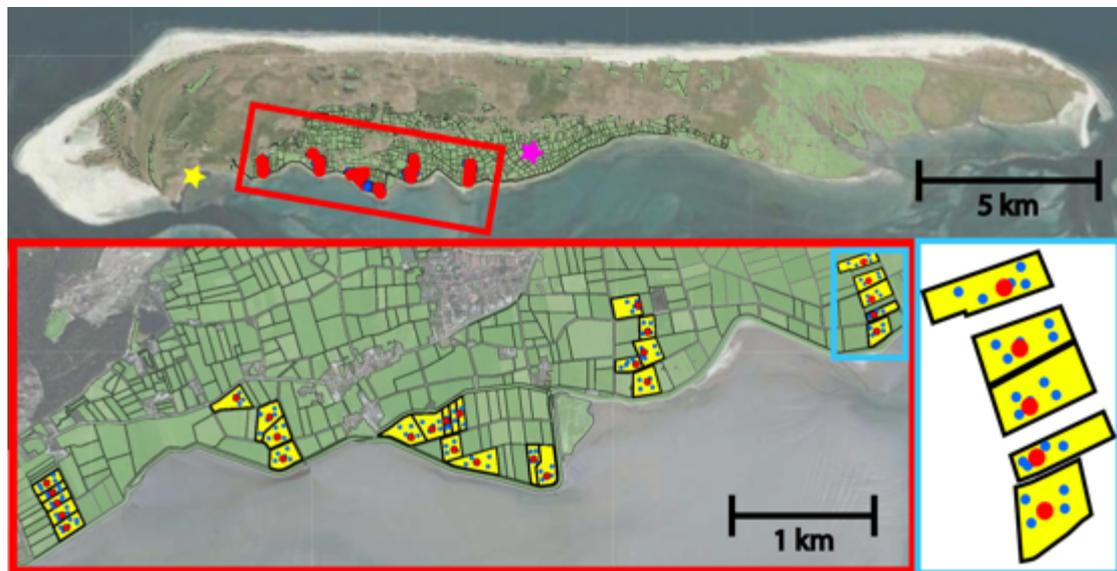


Figure S1: Study area on the island of Terschelling in the Dutch Wadden Sea. In total 27 fields were sampled, indicated in yellow. Each field hosted one exclosure station used for biomass sampling (red dots) and five stations (blue dots) where droppings were collected and grass height was measured. The yellow and purple star denote the location of tidal and meteorological measurement stations, respectively.

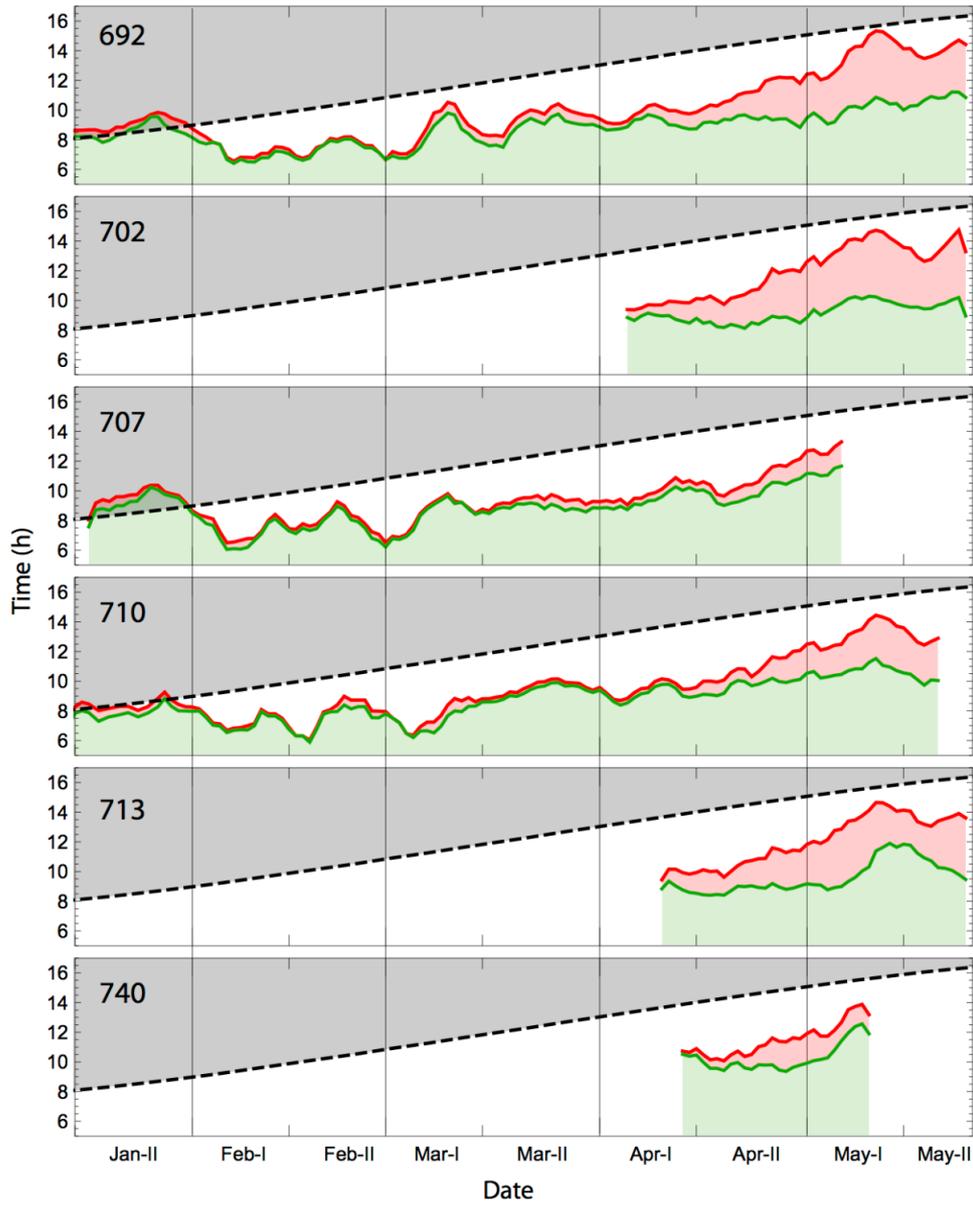
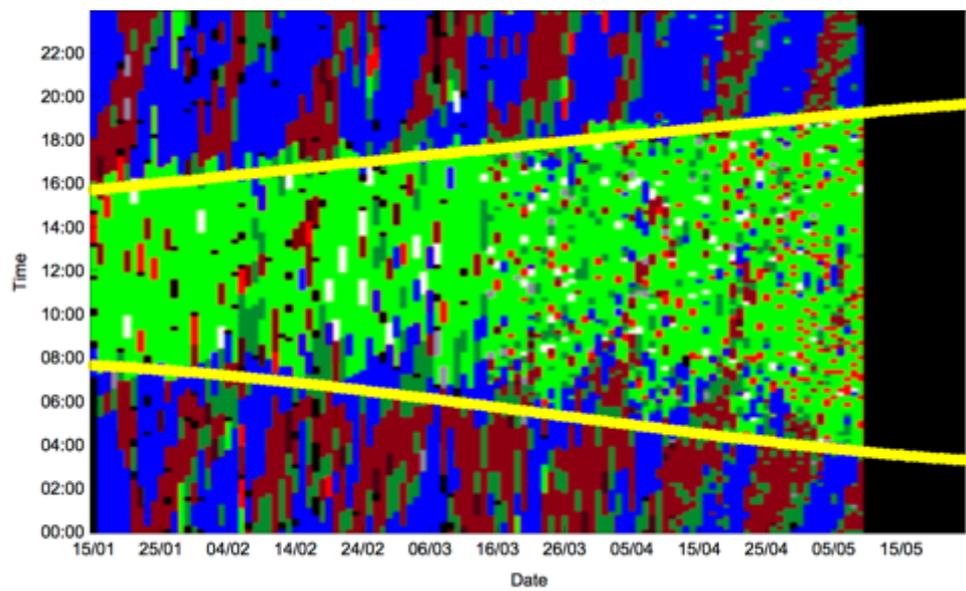
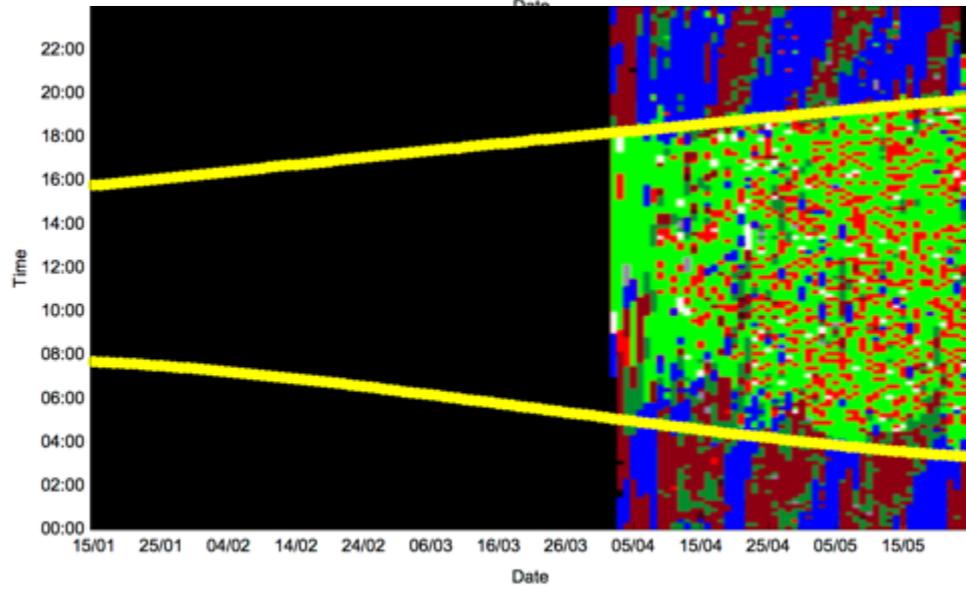
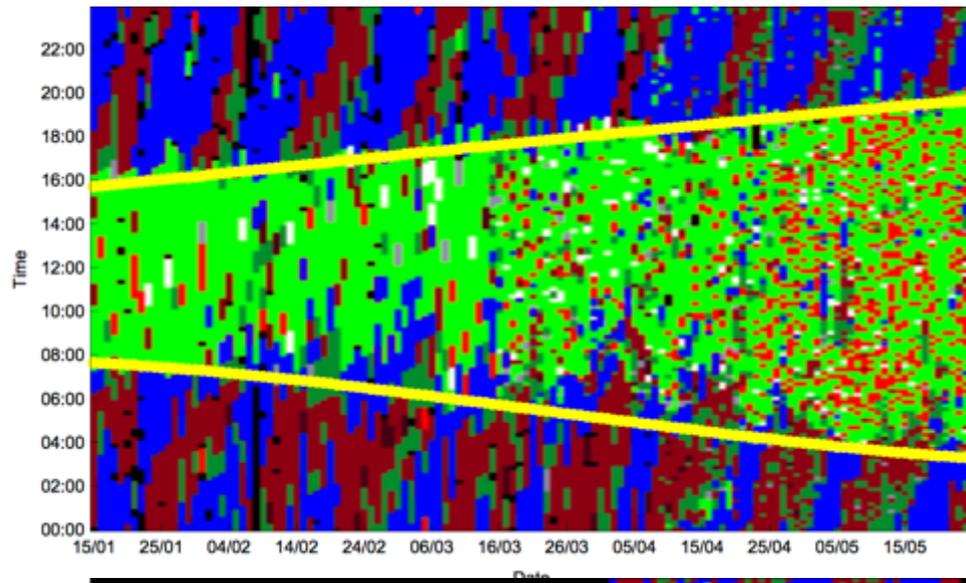


Fig. S2: Foraging activity time budget for all individuals, as in Fig. 2c of the manuscript



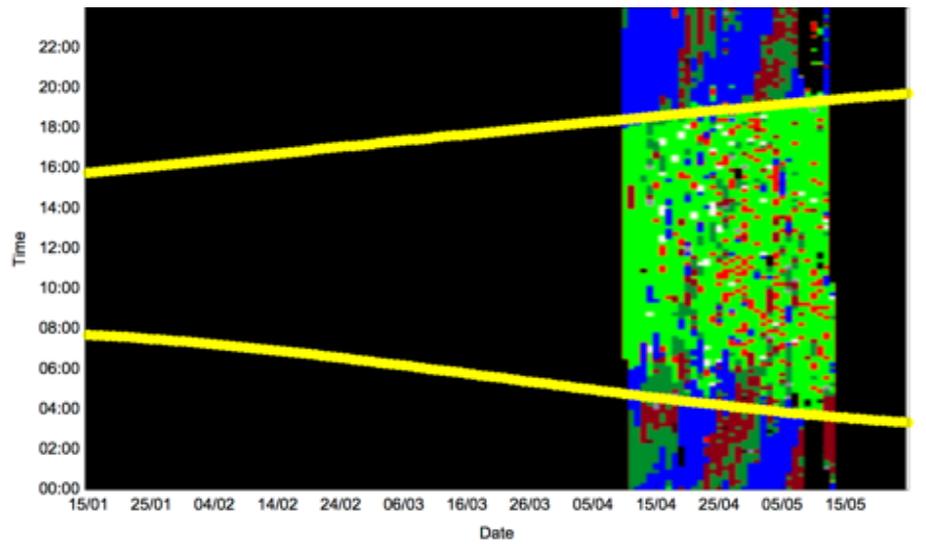
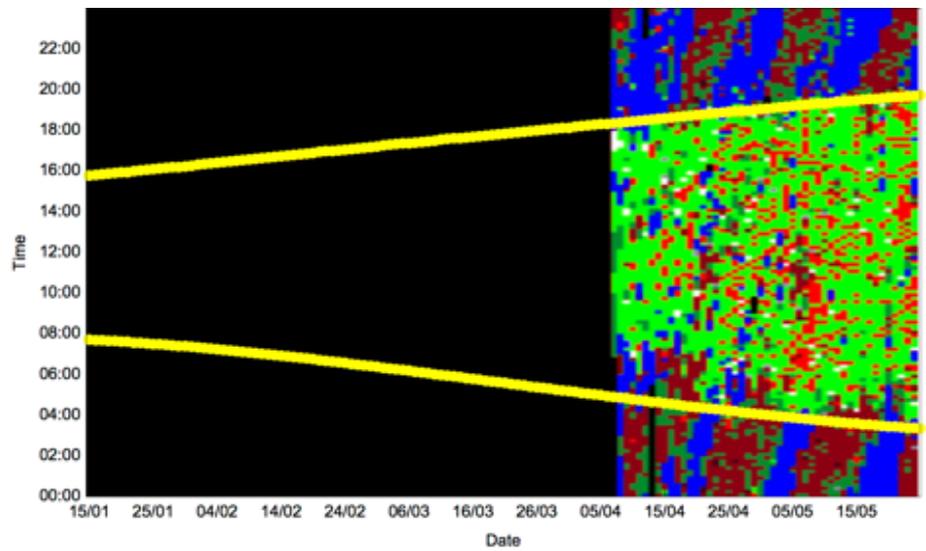
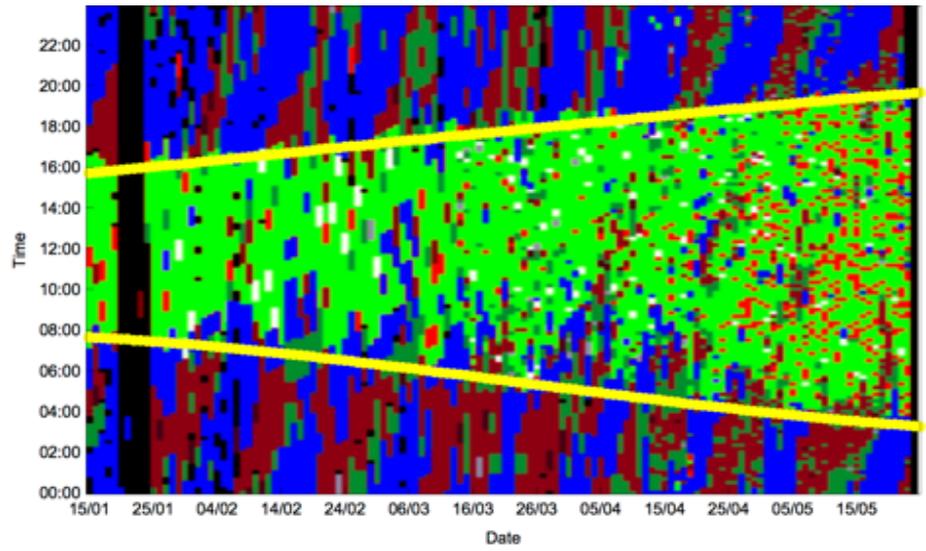


Fig. S3 a-f: Activity and location for all individuals, as in Fig. 2b of the manuscript.



Fig. S4: Dark-bellied brent geese grazing on Terschelling island (pastures of Strieperpolder, photo taken at the central transects indicated in lower left panel of Fig. S1) on 12 Apr 2012. Photo taken with a standard lens (no zoom) at the sea dike separating the pastures from the Wadden Sea (photo by Adriaan Dokter).

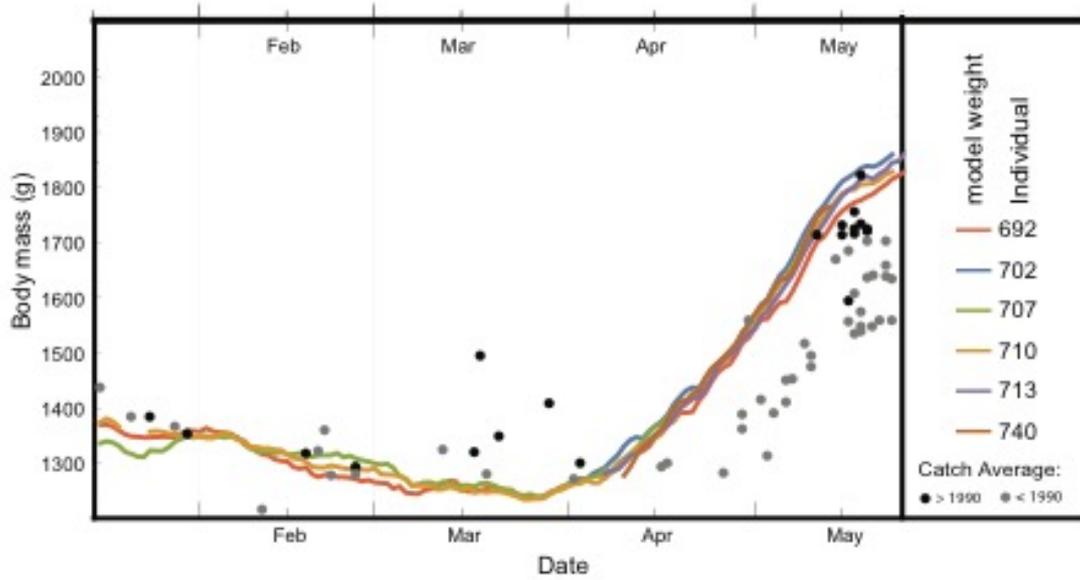


Fig. S5. Reconstructed weight changes during spring 2013 for six individual male brent geese. The trajectories are identical to Fig. 2e, but have been shifted along the vertical axis by the amount that the birds differed in body mass at capture (which were used as starting values for the trajectories). The curves highly overlap, which indicates that the time budgets on which the fuelling curves are based, were highly similar, and do not explain differences in fuelling trajectories.

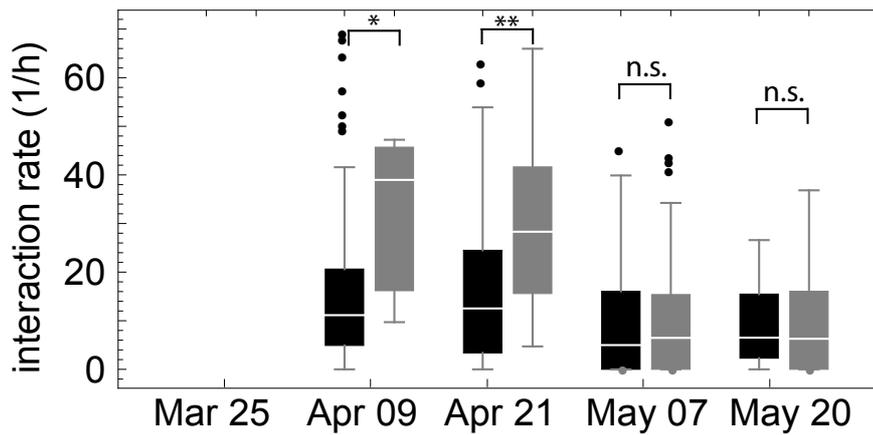


Fig. S6. Difference in interaction rate of Brent Geese at our pasture study site (black) and on a saltmarsh site (Schiermonnikoog, 60 km east of the study site) that was monitored simultaneously. Competition was quantified by scoring interactions between randomly picked focal individuals and other geese. We defined an interaction as a direct confrontation between two birds, ranging from threats with lowered head and neck to active chases with flapping wings, cf. (Stahl et al. 2001). Interactions were classified as wins, losses or draws (if no dominant bird in the interaction could be identified). We observed 441 interactions over 30 observation hours on saltmarsh, and 1415 interactions over 120 observation hours on pasture. Significance of pair-wise comparison between habitats for each period according to a Mann-Whitney U-test is indicated with stars (\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

## Supplementary tables

Table S1: Behavioural classification and BMR multipliers

accelerometer activity	location	inferred behaviour	b, BMR multiplier
$\alpha > 0.04$	grassland	Foraging & digesting	1.7
$\alpha < 0.04$	grassland	digesting	1.6
$\alpha < 0.04$	exposed mudflat	roosting	1.6
$\alpha > 0.04$	exposed mudflat	drinking, preening, nightly activities	1.7
$\alpha > 0.04$	on water	roosting	1.6
$\alpha < 0.6$	any	flying	13.4

Parameter b equals the BMR multiplier for the associated behaviour, taken from (Stahl 2001) and for flying from (Ladin et al. 2011). See appendix S2 and Figure S5 for thresholds defining accelerometer activity categories.  $\alpha$  expressed in units  $g_0$ , the the earth's standard gravity.

Table S2: Number of individuals caught at the study site from 2010-2016 in May

year	day	Total	Adult M	Adult F	Juvenile
2010	18	31	14	16	1
2011	17-19	127	56	48	23
2012*	15-16	30	14	10	6
2013	15-17	29	16	12	1
2014	13	67	24	20	23
2015	13-14	70	25	23	22
2016	18	23	12	11	0

\*Also a catch on Apr 3: 32 Adult M, 44 Adult F, 27 Juvenile. This catch was included for calculating the percentage juveniles.

## Appendix S1: Estimation of excretion rates

Droppings rates were estimated following (Dokter et al. 2017) using the R-package `intRvals`, available at [cran.r-project.org](http://cran.r-project.org). The methodology is briefly repeated here. We assumed dropping intervals  $x$  were to be excreted following a normal distribution  $N(\mu, \sigma^2)$ , with a probability density function  $\phi(x)$ :

$$\phi(x|\mu, \sigma^2) \sim N(\mu, \sigma^2) \quad (6)$$

with  $\mu$  the average dropping interval and  $\sigma$  its associated standard deviation. The probability density function  $\phi_{obs}$  of *observed* dropping intervals in a scenario where the chance to not observe a dropping is nonzero, will be a superposition of several peaks, at multiples of the fundamental mean dropping interval. Peak  $i$  will correspond to those intervals where  $i$  droppings have been missed consecutively. If  $p$  equals this chance of not observing a dropping, then the probability  $P(i)$  to miss  $i$  consecutive droppings equals

$$P(i) = p^i - p^{i+1} \quad (7)$$

The width of peak  $i$  will be broadened relative to the fundamental, according to standard uncertainty propagation in the case of addition, such that we may write for the observed PDF,  $\phi_{obs}$

$$\phi_{obs}(x|\mu, \sigma, p) = \sum_{i=1}^{\infty} P(i-1) \cdot \phi(x|i\mu, i\sigma^2) \quad (8)$$

In practice, values will be identical when the infinite sum is capped at a finite integer, in our analysis we ran the sum up to  $i=4$ . For a set of  $\{x_j\}$  intervals observed, we may calculate a log-likelihood

$$L(\mu, \sigma, p) = \sum_j \log \phi_{obs}(x_j | \mu, \sigma, p) \quad (9)$$

which we may maximize with respect to its parameters using standard numerical procedures, producing an estimate for the dropping interval  $\mu$ , associated standard deviation  $\sigma$ , and the chance of not observing a dropping event  $p$ . Dropping interval  $\mu$  was inverted to dropping rate  $r$ . We found that that the probability not to observe a dropping equalled  $p=0.20, 0.23, 0.27, 0.16$  and  $0.19$  for the five periods, respectively.

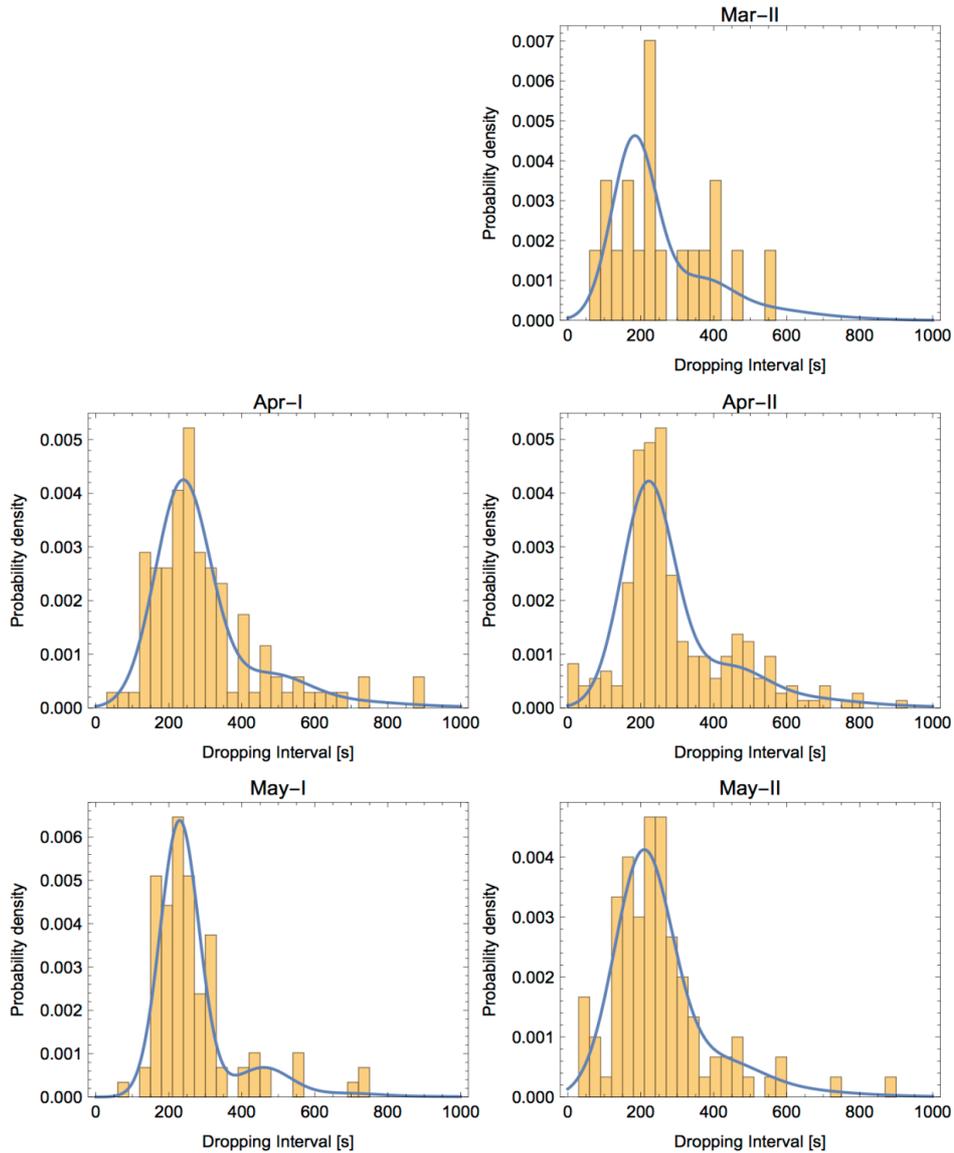


Fig. S4: Histograms of observed dropping intervals, and their fit to the probability density function of Equation 8 by maximum likelihood estimation (Equation 9).

## Appendix S2: Accelerometer classification of behaviour

As a measure of activity we used the accelerometer's vectorial sum of dynamic body acceleration  $\alpha$  (Qasem et al. 2012), defined as the root of the sum of the three acceleration variances for each axis:

$$\alpha = \sqrt{\sigma_x^2 + \sigma_y^2 + \sigma_z^2} \quad (10)$$

with  $\sigma_x$ ,  $\sigma_y$ ,  $\sigma_z$  the standard deviation of acceleration in the surge, sway and heave directions in units of  $g_0$ , the earth's standard gravity, and using a 20 Hz signal over 7/20 second. The probability density histogram for  $\alpha$  for birds located on the grasslands is shown in supplemental Figure S1. The peak at  $\alpha=0.015 g_0$  corresponds to cases where the bird is standing still, whereas the peak at  $\alpha=0.15 g_0$  corresponds to cases where the bird is actively foraging. We categorise a bird as inactive when  $\alpha < 0.04 g_0$  or active when  $\alpha > 0.04 g_0$  (see Table S1). The threshold was found by decomposing the distribution into two Gamma distribution components, equalling the point where these two components intersect at the same probability. Flying was detected using a threshold of  $\alpha > 0.6 g_0$ . We verified using 1 hour of video data on 4 GPS-tagged black brant (*Branta b. nigricans*) in captivity that the threshold in  $\alpha$  and sampling duration accurately distinguished inactivity from active behaviour (visually confirmed inactive resting  $\alpha = 0.015 \pm 0.01$ ).

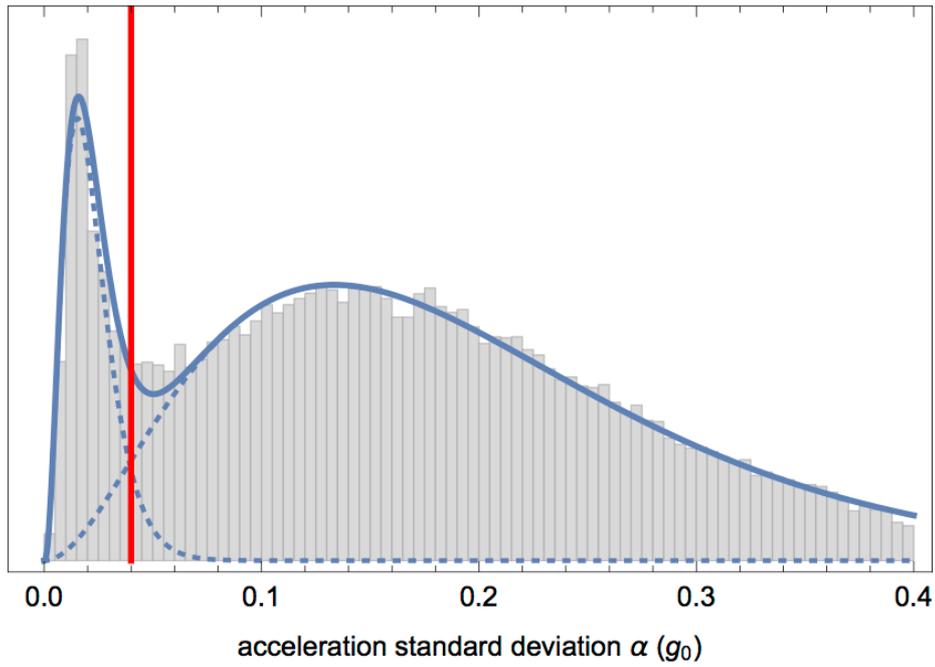


Fig. S5 Distribution of the tri-axial acceleration standard deviation  $\alpha$  for birds on the grasslands of Terschelling in spring 2013. The fit to the distribution (solid blue) is a least-squares decomposition into two Gamma distributions (dotted lines). The red vertical line indicates the threshold by which birds were classified as active or inactive.

### **Appendix S3: calculation of the scaled mass index: a body mass condition index corrected for structural size**

Both head length and wing length was available as structural size measurement of individual brent geese. Head length was measured from the tip of the bill to back of the head with using calipers, and wing stretched along a ruler with stop. Repeatability in these measures is very high. We followed the recommendation by (Peig and Green 2009) not to use a linear combination of structural size measurements computed by principal component analysis PCA, but only the log-transformed quantity that had the strongest correlation with log-transformed body weight. In our case this was head length for males (Pearson's  $r=0.47$  for head length, versus  $r=0.40$  for wing length) and wing length for females (Pearson's  $r=0.43$  for wing length, versus  $r=0.10$  for head length). We calculated the scaled mass index (SMI) recommended by (Peig and Green 2009), defined as

$$SMI_i = M_i \left[ \frac{L_0}{L_i} \right]^{b_{SMA}} \quad (11)$$

with  $M_i$  the mass of individual  $i$ ,  $L_i$  a linear body measurement of individual  $i$  (head length for males, wing length for females), and  $L_0$  an arbitrary scaling value for  $L$ , typically the arithmetic population mean of the linear body size measure.  $b_{SMA}$  is the slope of a secondary major axis (SMA) regression of  $\log(\text{body mass})$  against  $\log(L)$ . The mean (and standard deviation) of head length was  $L_0=93.8$  (3.0) for males ( $n=109$ ). The mean (and standard deviation) of wing length was  $L_0=332$  (63) for females ( $n=95$ ).

Using the `lmodel2` package in R we calculated both the SMA slope  $b_{SMA}$  and the conventional ordinary least squares (OLS) slope  $b_{OLS}$ . For males we found a slope

$b_{SMA}=2.4$  and  $b_{OLS}=1.1$  in a regression of  $\log(\text{body weight})$  on  $\log(\text{head length})$ . For females we found a slope  $b_{SMA}=3.74$  and  $b_{OLS}=1.6$  in a regression of  $\log(\text{body weight})$  on  $\log(\text{wing length})$ . After correction for structural size by Eq. 11, the difference in distribution (Kolmogorov-Smirnov test) and difference in medians (Mann-Whitney test) of the two distributions (adults versus juvenile's parents) remain significant at an  $\alpha=0.05$  significance level, showing our inferences are robust against structural size corrections. The difference between the two groups should thus be attributed primarily to a difference in body condition (fuel load), and not to a difference in structural size.

Interestingly, we find that when using the ordinary least squares slope  $b_{OLS}$  in Eq. 11 instead of  $b_{MSA}$ , we find the highest significance for all statistical tests quantifying the difference between the adult and juvenile's parents distributions, with p-values a factor 2-20 lower than for uncorrected body weights. Such a result can occur when SMA overestimates the true slope and OLS regression (using  $b_{OLS}$  instead of  $b_{SMA}$  Eq. 11) provides a better condition index. There is ongoing debate on whether SMA or OLS is the preferred regression method in the context of condition indices (Warton et al. 2006; Peig and Green 2009). Given that the repeatability of head and wing length measurements is often higher than the repeatability of body mass measurements in geese (Larsson and Forslund 1991), it may well be that in this species the measurement error in weight is much larger than in body length, making OLS possibly more appropriate. Notwithstanding these results we only report the more conservative p-values for body mass corrected using SMA regression.

## Appendix S4: Integrating data to reconstruct energy balance and fuelling

We will denote the assimilated (metabolisable) energy over a certain time interval  $i$  as  $A_i$ . During periods of constant weight under thermoneutral conditions, the assimilated energy equals the existence energy  $E_i$ , which includes both basal metabolism and energy for locomotion and other activities. We define the thermoregulatory expenditure  $T_i$  as the energy required to maintain the bird's body (or any other object with identical shape, heat capacity and plumage isolation) at 40 °C, according to the physical laws of heat and radiation transfer. Finally, productive energy  $P$  is the energy assimilated above the amount needed for existence and thermoregulation, which is converted to the bird's change in body stores  $W_i$  with a cost of mass change  $\gamma$  (kJ/g). Therefore, for a time interval  $i$  of duration  $t_i$  (corresponding to one GPS fix), we may write (Blaxter 1989):

$$\begin{aligned} P_i &= A_i - \max[E_i, T_i] \\ W_i &= P_i/\gamma \end{aligned} \tag{4}$$

assuming that the heat generated in activities can be used in thermoregulation, such that only when thermoregulatory expenditure  $T_i$  exceeds the existence energy  $E_i$ , a bird pays additional thermoregulation costs (Paladino and King 1984) (the max function selects the argument with largest value). For daily sets of  $A_i$ ,  $E_i$ ,  $T_i$ ,  $P_i$  and  $W_i$  values we calculated daily sums  $DA$ ,  $DE$ ,  $DT$ ,  $DP$  and  $DW$ , respectively, as in  $DA = \sum_i A_i$ , with  $i$  over all  $A_i$  values of an individual within a day.

*Assimilated energy A and existence energy E: remote classification of behaviour and digestion*

Assimilated energy ( $A_i$ ) and existence energy ( $E_i$ ) were derived from time budgets calculated from an accelerometer-based behavioural classification (Table S1), combined with the energy assimilation rate  $R_{assim}$ , as described above. Behaviour was

inferred from the accelerometer-data collected with each GPS fix and habitat (using a tidal reconstruction), as summarised in supplementary Table S1. Existence energy was calculated using behaviour-specific multipliers of the basal metabolic rate (BMR). Except for flying, most behaviours are very similar in terms of energy expenditure, see e.g. (Stahl 2001). We use the BMR multipliers measured by (Stahl 2001) as calibrated by heart rate measurements, see Table S1.

$$\begin{aligned} A_i &= d_i \cdot R_{assim} \cdot t_i \\ E_i &= b_i \cdot BMR \cdot t_i \end{aligned} \quad (5)$$

with  $d_i$  a binary variable (0/1) which describes whether birds were actively digesting,  $R_{assim}$  as in Eq. (1),  $t_i$  the time interval associated with fix  $i$ ,  $b_i$  the BMR multiplier associated with the classified behaviour, and BMR the basal metabolic rate. Each time interval  $i$  (see Fig. 3a) equals the time between temporal midpoints of the fix with the preceding and following fix.

Birds were assumed to be actively digesting ( $d=1$ ) as soon as birds started active foraging on the grasslands. Digestion was assumed to continue during inactive pauses on grasslands, as long as these periods lasted less than one hour, i.e. shorter than the average retention time (Prop and Vulink 1992). Digestion was assumed to stop ( $d=0$ ) during pauses longer than one hour. We further assumed that any delay in the startup of the digestive process on an empty stomach, associated with retention in the digestive tract, was balanced by an equal amount of continued digestion after stopping active foraging, such that explicit bookkeeping of these time lags was not required.

To determine whether birds were on water, we used a bathymetric map of the Dutch Wadden Sea (cycle 5 map at 20 m resolution) and tidal water heights (every 10 minutes) provided by Rijkswaterstaat, Ministry of Infrastructure and the Environment. Mudflats were assumed to be flooded when the bathymetric height at the birds position was below

the water height measured by the tidal station West-Terschelling (53.36305N 5.22003E, see supplementary Fig. S1).

We used the value  $BMR_{ref}=5.62$  W by (Stahl 2001), since our thermoregulation model and activity-specific BMR multipliers were fitted against this measured BMR value under the assumption of thermoneutrality. Intra-individual allometric scaling is not expected to follow Kleiber's law ( $3/4$  mass exponent), but to be proportional to mass, which seems consistent with the available intra-individual data for birds (Daan et al. 1989; Kvist and Lindström 2001; Maino et al. 2014). We therefore assumed BMR to vary according to  $BMR=m*BMR_{ref}/m_{ref}$ , with  $m_{ref}=1564$  g the weight of the individual during BMR lab measurements (Stahl 2001).

#### *Thermoregulatory expenditure T: heat transfer modelling*

Thermoregulatory expenditure was calculated according to the model by Cartar & Morrison (1997). The model calculates the maintenance metabolic expenditure ( $T_i$ ), defined as the energy in the form of heat required to keep the bird's body at an equilibrium temperature of 40 °C. It is calculated using physical heat transfer equations as a function of body mass, ambient temperature, wind speed at 10 m standard height and global radiation (as measured by a pyranometer) at the time of each GPS fix  $i$ . We used an identical parametrisation as for arctic geese by (Baveco et al. 2011), with two study-specific adjustments: (1) we used the plumage resistance (798 s/m) measured specifically for a brent goose under thermo-neutral conditions (Stahl 2001). (2) we extrapolated wind speed from 10 m standard measurement height to the level of the bird using a habitat-specific roughness length  $z_0$  (Cartar and Morrison 1997; Baveco et al. 2011), which is the height where a logarithmic wind profile becomes theoretically zero. We used  $z_0=0.005$  as the standard roughness length used by the World Meteorological

Organisation (WMO) for mudflats (WMO 2008), where birds spend the night and pay most thermoregulatory costs. The wind speed at bird level (0.15 m) then equals a fraction  $\log(0.15/z_0)/\log(10/z_0)=0.45$  of the 10 meter wind. Meteorological parameters were obtained for meteorological station 'Hoorn Terschelling' (53.391205 N, 5.345746 E, WMO index number 06251, see supplementary Fig. S1) located in the study area.

#### *Cost of mass change $\gamma$*

We used a cost of mass change  $\gamma$  determined for fuelling shorebirds in captivity  $\gamma=45.66$  kJ/g (Kersten and Piersma 1987). The composition of body stores of brent geese has also been determined by carcass analysis, which indicate these stores represent an energetic value of 25.5 kJ/g (Prop and Deerenberg 1991). This estimate however does not include any costs for tissue synthesis, nor for building muscle capacity (Lindström and Piersma 1993), and therefore represents a lower limit to the true costs of mass change.

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