Outflying climate change

Optimal timing of migratory geese breeding in a warming Arctic

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Keeping up with early springs: can avian herbivores advance fuelling under climate change?

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ABSTRACT

Under climate warming the onset of spring is advancing, and species need to adjust their reproduction phenology to keep up with these early springs. Migratory species therefore need to advance their migratory schedules, which they could achieve by fuelling for migration earlier. Advancement of fuelling may be constrained early in the season by high energy expenditure in cold winter conditions and little time available for foraging under short day lengths. We investigate whether Arctic-nesting migratory barnacle geese *Branta leucopsis* have potential to advance fuelling, by comparing their foraging effort with resident barnacle geese, which have abandoned their migratory strategy and currently breed in their former wintering grounds, where they have advanced laying dates to match the local onset of spring. We therefore expect resident geese to also have advanced fuelling, but only if they are not constrained in time or energy to do so. We equipped migratory and resident barnacle geese with GPS-trackers including accelerometers to record time budgets and grazing time, which we combined with environmental data to quantify energy expenditure. We show that geese adjusted grazing time to available foraging time, and increased grazing time with increasing day length, available moonlit hours during the night and higher thermoregulation costs. Both migratory and resident geese started to increase grazing time with longer day lengths from mid-February. However, geese appear to have leeway to advance fuelling by increasing grazing time early in the season, as they do not graze during all moonlit nights, and can increase grazing time when facing high energy expenditure. This suggests there is scope for advancing fuelling, but the current onset and rate of fuelling in early spring is not triggered by a release from environmental constraints, but by photoperiod. Resident populations of barnacle geese may still use the same cues for the onset of fuelling as their migratory counterparts, while this has in fact become outdated in relation to their advanced reproductive season. Current climatic conditions may not provide the need to advance fuelling, but an advancement of fuelling under future climate warming may be hampered by cue sensitivity rather than environmental constraints.
Chapter 6

Introduction

Animals in seasonal environments can optimise reproduction success by matching reproduction timing with seasonal peaks in food availability (van Noordwijk et al. 1995). As peaks in food availability typically occur early in the season, and earlier-born offspring have a longer period to grow, early reproducing individuals typically experience highest reproductive success. Adults themselves, however, may benefit from breeding later in the season, as a low availability of food early in the season constrains them from getting into optimal condition for breeding. Food supply for the female has been found to be one of the proximate drivers of laying date, with higher food availability allowing animals to reproduce earlier (Meijer & Drent 1999; Drent 2006). While offspring greatly benefits from hatching at the peak of food availability and quality, adults may need to use the same food peak to accumulate reserves for laying eggs.

Migratory animals escape this problem by making use of multiple food peaks along their flyway, as they migrate along a gradient of delayed onset of spring (a “green wave”; Drent et al. 1978; van der Graaf et al. 2006; Shariatinajafabadi et al. 2014). This allows adults to prepare for reproduction during migration, using peaks in food quality in the wintering and staging grounds, while their offspring benefits from a peak in food availability on the breeding grounds (van der Graaf et al. 2006). Under current climate warming the onset of spring is advancing, and with that the timing of peak food availability on the breeding grounds (Tulp & Schekkerman 2008; van Asch et al. 2012; Doiron et al. 2015; Lameris et al. 2017b). To keep a match between chick hatching date and peak food availability, animals are expected to advance their timing of reproduction (Visser et al. 2012). Mismatches between the timing of hatch and peak food availability have been found to have far-reaching consequences for offspring growth, survival and eventual fitness (Visser et al. 2004; Doiron et al. 2015; van Gils et al. 2016). To advance laying dates, migrants should advance arrival on the breeding grounds (Both & Visser 2001), and with that, departure from the wintering grounds (Ouwelhand & Both 2017; Schmaljohann & Both 2017). However, an advancement of departure may only be possible if animals can come into condition for long migration flights earlier in the season, and thus advance fuelling for migration and reproduction (Lameris et al. 2017c).

An animal can initiate fuel deposition by increasing its energy intake so that it exceeds its daily energy expenditure, known as hyperphagia (Lindström 2003). The onset and rate of fuel deposition can be constrained by high energy expenditure (e.g. in cold winter conditions; Owen et al. 1992), time availability for foraging (e.g. when foraging is only possible during daylight conditions; Owen et al. 1992) or digestive capacity (e.g. when food is of low quality; Gauthier and Bédard 1992; Prop and Vulink 1992). On the other hand, animals can choose to postpone fuelling until shortly before migration (Ebbingeg & Spaans 1995), as they are more susceptible to predators when carrying larger fuel loads.
Advancement of fuelling under early springs

(Hedenström 1992; Witter & Cuthill 1993). In winter, when fuelling is constrained by cold conditions, short day length and low food quality, animals may have to forage at maximum intensity to balance energy intake with expenditure. In early spring, when animals become less constrained, they can initiate fuelling by keeping up maximum foraging intensity, or by increasing foraging time in phase with a certain cue, such as increasing photoperiod or temperature. When the need comes to advance departure for migration under a warming climate, animals can therefore only advance fuelling if they do not already hit the ceiling of energy intake early in the season (Herbers 1981; Owen et al. 1992; Jeschke & Tollrian 2005). At the same time climate warming can ameliorate conditions for fuelling early in the season, by milder winter temperatures which lower energetic costs for thermoregulation, and which may contribute to an improved food quality (although this can also be ascribed to the increased use of chemical fertilizers; van Eerden et al. 2005). However, the time available for foraging during daylight hours, which is not affected by climate warming, may still constrain an advancement of fuelling early in the season. Even if animals are not constrained to advance, their flexibility to advance may be inherently linked to the cues which they currently use to time the onset of fuelling, and whether these cues change under climate warming (Knudsen et al. 2011; McNamara et al. 2011).

In this paper we study whether Arctic migratory barnacle geese *Branta leucopsis* are constrained to advance the onset of fuelling in early spring in their wintering grounds. As migratory geese may currently not be driven to initiate fuelling at the earliest possible day, we investigate this by making use of a unique comparison between the migratory population and a resident population of barnacle geese, of which we expected the latter to have advanced their fuelling already in response to advanced laying dates. Migratory and resident populations co-occur along the North Sea coast of the Netherlands and Germany and share the same potential constraints for fuelling in their wintering habitat, but differ in their annual cycles, as resident geese initiate laying in late April, where migratory birds depart on a 3000 km migration to their Arctic breeding grounds in mid-May. While migratory geese may need to fuel more to finance both migration and reproduction, resident geese are driven to initiate fuelling at the earliest possibility, as they currently already nest too late to avoid a mismatch between chick hatching and peak food availability (van der Jeugd et al. 2009). By remotely measuring daily time budgets in free-living barnacle geese, we ask whether the grazing effort (measured as grazing time) in barnacle geese is regulated by 1) time available for foraging, and 2) by energy expenditure, and how these factors together determine the onset fuelling, and how the differs between populations.
Chapter 6

Methods

We used data from GPS-trackers and accelerometers deployed on free-living barnacle in the spring of 2015 (migratory geese, n= 23 individuals) and 2017 (resident geese, n= 12 individuals), from which we derived their behaviour and calculated daily time budgets and daily grazing time. We gathered data on available foraging time for geese during the day (daylight hours) and the night (moonlit hours). By combining time budgets with climate data and behaviour-specific energy expenditure, we modelled daily thermoregulation costs and total energy expenditure. Although we use data from different years for different populations, the close similarity in climatic conditions in these two years (Figure S6.1) allow for a comparison between populations.

Study populations

Barnacle geese are originally Arctic migratory birds, and the complete population is subdivided in three flyway populations, breeding on Eastern Greenland, Svalbard and along the Barents Sea coast (Madsen et al. 1999). The population in the Barents Sea region migrates northwards in spring from wintering grounds in North-Western Europe, using staging grounds in the Baltic Sea, the White Sea, Kanin peninsula and the Barents Sea (Eichhorn et al. 2006; Figure 6.1a). This population has in past decades expanded its breeding range and has started nesting in former temperate staging and wintering sites. Migratory Arctic breeders and resident temperate breeders now spend the winter together in the coastal region of the North Sea (the Netherlands and Germany). Foraging habitat consist of both manmade, agricultural pastures and natural habitats, mostly salt- and freshwater marshes (van der Graaf et al. 2006). The migratory population of barnacle geese stage longer and depart on spring migration in mid-May (Eichhorn et al. 2009). These geese then initiate nesting on their Arctic breeding grounds shortly after snowmelt in early June (Drent et al. 2007).

We study migratory and resident barnacle geese from an Arctic and temperate breeding colony. The Arctic breeding colony is located on the edge of the Kolokolkova bay, northern Russia (68°35’N, 52°20’E; van der Jeugd et al. 2003; Fig 1A). The temperate breeding colony is located in the Delta region (Westplaat Buitengronden), in the South-Western part of The Netherlands (51°47’N, 4°08’E; van der Jeugd et al. 2009; Fig. 1C). Geese from both populations forage along the North Sea coast in winter and early spring, with migratory birds mostly residing along the Wadden Sea coast (Fig. 1B), while resident birds reside close to their breeding colony in South-West Netherlands, ranging maximally 50 km from the colony (Fig. 1C). We study migratory and resident barnacle geese from an Arctic and temperate breeding colony. The Arctic breeding colony is located on the edge of the Kolokolkova bay, northern Russia (68°35’N, 52°20’E; van der Jeugd et al. 2003; Figure 6.1a). The temperate breeding colony is located in the Delta region (Westplaat Buitengronden), in the South-Western part of The Netherlands (51°47’N, 4°08’E; van der
Jeugd et al. 2009; Figure 6.1c). Geese from both populations forage along the North Sea coast in winter and early spring, with migratory birds mostly residing along the Wadden Sea coast (Figure 6.1b), while resident birds reside close to their breeding colony in South-West Netherlands, ranging maximally 50 km from the colony (Figure 6.1c).

Figure 6.1: Overview of the areas where geese resided during the study period: (A) the migration route of Arctic-breeding migratory barnacle geese (orange lines) which breed in a colony at the Kolokolkova Bay, along the Barents Sea coast (orange star); (B) foraging locations of migratory birds (orange dots) and resident birds (blue dots) in their wintering grounds along the North Sea; (C) foraging locations of resident barnacle geese (blue dots) in the Delta region of The Netherlands, which nest in a local colony (blue star).

Attachment of GPS-trackers
Of the migratory population, we captured 40 adult female barnacle geese on the nest at the colony at the Kolokolkova Bay, Russia, during the incubation period in late June – early July 2014. Of the resident population, we captured 19 adult female geese on the nest in the colony at the Westplaat Buitengronden, during the incubation period in late April – early May in 2016. At capture, we measured birds’ body mass and size, applied engraved coloured plastic leg rings and fitted the birds with 19 gram UvA-BiTS GPS-trackers (Bouten et al. 2013). We attached the GPS-trackers with a 16-gram Teflon harness
(Lameris et al. 2017a). Although harness attachments can have negative effects on bird performance (Lameris & Kleyheeg 2017), we found only minimal effects on survival, migration and reproduction of tagged birds (Chapter 4). For the migratory population, GPS-trackers were programmed to collect GPS positions at an interval of 15 to 30 minute in the wintering region. For the resident population, GPS-trackers were programmed to collect GPS positions at an interval of 30 to 60 minutes in the wintering range and at an interval of 5 minutes in the breeding colony. Following each GPS-fix, 10 samples of tri-axial acceleration data were collected at 20 Hz. In the summer of 2015 at the Kolokolkova Bay, and the spring of 2017 at the Westplaat Buitengronden, we could remotely download data from GPS-loggers using Zigbee wireless antennas and base station (Bouten et al. 2013). This resulted in 35 complete spring tracks, 23 for the migratory population and 12 for the resident population. We used GPS and accelerometer data from migratory birds up to the onset of migration (up to the last position in the Wadden Sea area), and from resident birds until they started laying eggs (as measured for individual birds in the field, see (van der Jeugd et al. 2009) for methods).

**Time budgets**

From tri-axial accelerometer data collected by our GPS-trackers time budgets were calculated for individual geese from both populations. A tri-axial accelerometer measures movement acceleration (g-force) with respect to the earth’s gravitational field in three directions: surge (x), sway (y) and heave (z) (Shamoun-Baranes et al. 2012, 2016). We calibrated a machine-learning model to classify behaviours from these accelerometer data. We trained and validated the model with a dataset of accelerometer data of filmed behaviours from 8 barnacle geese kept in captivity at our research facilities in Wageningen, the Netherlands in April 2014 (approved by Animal Welfare Committee, protocol NIOO 14.01). With the machine-learning model we were able to distinguish grazing, flying, inactive and active behaviour (see supplementary materials for full methods).

To make datasets with different intervals between GPS-fixes comparable, we resampled all data to include only one fix every 30 minutes. We considered the time interval between one and the following GPS-fix as the duration of the sampled behaviour. From these data we generated daily time budgets for every individual bird (Figure 6.2a).

**Day length, weather and land use data**

For every day in 2015 and 2017 we collected data on sunrise and sunset for the locations of individual geese using the NOAA sunrise and sunset calculator tool (Cornwall et al. 2014) via the function ‘sunrise.set’ in the R package ‘StreamMetabolism’ (Sefick Jr 2009). We collected data on moonrise, moonset and fraction of moon visible for every day using an average location for each population (migratory: 53°52’N, 7°18’E; resident: 51°76’N, 4°10’E) in the USNO moonrise and moonset calculator (Naval Meteorology and Oceanography
Advancement of fuelling under early springs

From these data we calculated hours of day length, and the hours per night during which the moon was visible. Data on daily average temperature, cloud cover, U and V wind components at 10 m and long- and short-wave radiation were collected at 6 hourly interval for locations of individual geese from the NCEP reanalysis numerical weather model (Kalnay et al. 1996), using the R package ‘RNCEP’ (Kemp et al. 2012). For every location where a bird was grazing, we categorized locations by land use, using the CORINE dataset from 2006 (Büttner et al. 2004; Büttner & Kosztra 2007), and distinguished between agricultural area (arable land, pastures and heterogeneous agricultural areas) and natural areas (natural grassland, inland marshes and salt marshes). For 6.5% of the fixes where a bird was classified as grazing, we encountered other classes of land use. With the help of Google Earth (Google, 2017), we determined whether this was due to an erroneous land cover classification (5.7%), after which we corrected this by hand, or whether the grazing behaviour was classified incorrectly (0.8%). The latter was often the case when birds were sitting still on open sea, as waves would result in an accelerometer signal similar to grazing, and for these points we corrected the behaviour to resting (Shamoun-Baranes et al. 2011, 2016).

Modelling costs of thermoregulation and activity

As resident geese spent the winter and early spring slightly more to the south than migratory geese (Fig. 1) where they experience a somewhat warmer winter climate, the energetic costs of thermoregulation could also be less. This could simultaneously affect their grazing effort. We aimed to investigate whether differences in grazing time between resident and migratory could be explained by differences in energy expenditure. We thus modelled thermoregulation and activity costs by combining time budgets derived from accelerometer data and local weather data in a bio-energetics model. For one GPS-fix (i) every 30 minutes, we calculated the energy needed for existence \( E_i \), thermoregulation energy costs \( T_i \), and the total energy costs \( TE_i \). We calculated energy costs for the entire season for a 1600 gram weight goose, as winter weights are not known to differ between populations and equal weight facilitates comparisons.

We calculated existence energy \( E_i \) for every GPS-fix \( i \) as:

\[
E_i = BMR \times b_i \times t_i
\]  

(6.1)

Where \( BMR \) is the basal metabolic rate of an individual bird (4.853 W for a 1600 g barnacle goose, following Daan et al. 1989; Nolet et al. 1992), \( b_i \) the behaviour-specific multiplier (inactive = 1.5, active = 1.9, grazing 1.6; Stahl et al. 2001) for behaviours determined using accelerometer data (see above) and \( t_i \) is the time interval from the GPS-fix \( i \) until the following GPS-fix \( i + 1 \). As the costs of flight depend on wind conditions, and GPS-fix intervals of 30 minutes cannot detect short periods of flight, we used a different method to
Thermoregulation costs $T_i$ are the costs to maintain a relatively constant body temperature when environmental temperature drops below the thermoneutral zone. We follow the model developed by Cartar and Morrison (1997), which calculates the thermoregulation costs $T_i$ as a function of body mass, ambient temperature, wind speed at 10 m and global radiation at $i$. Our parameterisation was similar to Baveco et al. (2011), but we used the plumage resistance measured for barnacle geese (van der Graaf et al. 2001) and we extrapolated the wind speed from 10m height to the level of the bird (15 cm height) using roughness length $z_o$ for open terrain / lower salt marsh (0.01 meter; de Vries 1999). We assumed that heat generated during activities can be used for thermoregulation (Paladino & King 1984), and only when $T_i > E_i$ the bird pays additional thermoregulation costs. Total energy costs were calculated as:

$$TE_i = (T_i < E_i \rightarrow E_i) \land (T_i > E_i \rightarrow T_i + E_i)$$

(6.2)

**Statistics**

We aimed to test 1) how time available for grazing and energy expenditure affected grazing time during day and night over the season; 2) when geese started to fuel body reserves by an increase of grazing time and a decrease in energy expenditure; and 3) how these aspects differed between populations. For analyses where we compared populations, we restricted our data to the period up to mid-April (day number 100), as after this date resident geese started to decrease their grazing time. This could partially be due to laying dates which occurred soon after this date, but also by increased disturbance in the colony caused by human activities.

We tested relationships by running linear- mixed models using the package “lme4” in R 3.0.2 (R Core Team, 2014). Models with combinations of variables were compared using Akaike’s information criterion (AICc; (Burnham & Anderson 2002)) and we chose the model with the lowest AICc value as our final model. The best performing models are summarized in the supplementary material. We tested for significance of fixed factors by comparing the final model with a reduced model in which the fixed factor was absent, using a likelihood ratio test. To test at which point in time total grazing time, thermoregulation and total energy expenditure started to increase / decrease, we determined breaking points for a segmented linear mixed model (Bacon & Watts 1971), where we selected the breaking point which led to the maximum likelihood estimates for all parameters in the model. We determined breaking points for populations separately, but also for the combined dataset including both populations.

We tested what affected grazing time during daytime and night-time by fitting a linear mixed model with individual birds as a random factor, and included fixed factors day length, habitat, population (migratory vs resident) and the interaction between day
length and population (for daytime models); hours of moonlight, habitat, population, date, date^2 (the quadratic term of date), the interaction terms of date and population and date^2 and population (for night-time models). We tested how energy expenditure affected total grazing time (day and night combined) by fitting a similar model including fixed factors hours of moonlight, day length, population and thermoregulation costs / total energy costs (analysed in separate models).

To test differences in grazing time and energy expenditure, we split our datasets, on the basis of the date found as the breaking point for populations combined, into a ‘pre-fuelling period’ (before the breaking point) and a ‘fuelling period’ (after the breaking point). We made a separate split for the breaking point in grazing time (determined at February 14th) and the breaking point in total energy costs (determined at February 7th). We then tested whether thermoregulation costs, flight costs, flight time and total energy costs differed between populations in the pre-fuelling period by running linear mixed effect models including individual birds as a random factor and population and date as fixed factors. We tested the rate of increase / decrease over time and differences between populations in the fuelling period by running linear mixed effect models for grazing time, thermoregulation costs and total energy costs including individual birds as a random factor and population and date as fixed factors.

**Results**

**Grazing time and available foraging time**

Geese mostly grazed during daylight hours, and initiated long bouts of grazing shortly after dawn, continuing grazing until dusk, after which they took long periods of rest (Figure 6.2a, b). Geese increased daytime grazing from the start of the season simultaneously with more daylight hours, at higher rate in the migrant population (regression coefficient migrants $\beta = 33.87 \pm 7.41$ minute increased grazing per hour of day length; residents $\beta = 29.22 \pm 1.51$. day length; $\chi^2 = 2039.8, p < 0.001$; interaction day length and population: $\chi^2 = 9.5, p = 0.002$; Figure 6.2c, d). Daytime grazing of both populations was at a relatively stable proportion of day length over the complete period which differed between migratory and resident populations (migrants, $\beta : 0.66 \pm 0.10$; residents; $\beta = 0.61 \pm 0.11$ proportion of day length; $\chi^2 = 153.1, p < 0.001$; Figure S6.2).

Night-time grazing was mostly possible under moonlight conditions, as geese spent a maximum of 4 – 6 hours grazing in nights around full moon, and night-time grazing increased with hours of moonlight ($\beta = 4.32 \pm 0.29$ minute per hour of moonlight, $\chi^2 = 221.1, p < 0.001$; Figure 6.2c, d). Night-time grazing initially decreased over the season (migrants $\beta = 2.75 \pm 0.13$ minute decrease grazing per day, residents $\beta = 1.32 \pm 0.26$; day number: $\chi^2 = 466.3, p < 0.001$; interaction day number and population: $\chi^2 = 15.1, p < 0.001$) and was most intensive during moonlit nights in January – February, but increased again
later in the season as geese started to graze early in the morning, shortly before sunrise (migrants \( \beta = 0.019 \pm 0.0009 \) minute increase grazing per squared day, residents \( \beta = 0.016 \pm 0.0020 \); day number squared: \( \chi^2 = 493.6, p < 0.001 \); interaction day number squared and population: \( \chi^2 = 2.2, p = 0.136 \); Figure 6.2a, b).

Grazing time also differed between habitats, and in natural habitats geese spent 51 ± 6 minutes more grazing during daytime (\( \chi^2 = 78.6, p < 0.001 \)); and 26 ± 4 minutes more during nigh-time (\( \chi^2 = 42.9, p < 0.001 \)) compared to agricultural habitats (Figure 6.2c, d).

\[ \chi^2 = 30.0, p < 0.001 \]

\[ \chi^2 = 23.4, p < 0.001 \]

The close link between expenditure and natural habitats (dark green / dark blue). The black shadowed area shows night-time hours, the white area shows daytime hours, yellow bars show the time during which the moon was visible.

**Grazing time and energetic costs**

Geese adjusted their grazing time to daily fluctuations in thermoregulation costs (\( \beta = 0.16 \pm 0.03 \) minutes increase in grazing per kJ of thermoregulation costs; \( \chi^2 = 30.0, p < 0.001 \)) and total energy costs (\( \beta = 0.06 \pm 0.01 \) minutes decrease in grazing per kJ of thermoregulation costs; \( \chi^2 = 23.4, p < 0.001 \)). The close link between expenditure and
grazing time is also highlighted by differences between populations. Migratory geese spent more total grazing time than resident geese during January – mid February (up to day 36) (migrants; $\beta = 437 \pm 11$ minutes; residents; $\beta = 384 \pm 18$ minutes; $\chi^2 = 45.7, p < 0.001$, Figure 6.3a, b). In this same time period, migratory geese also experienced higher thermoregulation costs ($T$)(migrants; $\beta = 835.8$ kJ per day; residents; $\beta = 824.0$ kJ per day, $\chi^2 = 7.5, p = 0.006$), caused by stronger winds in their wintering region (migrants; $\beta = 3.44$ meter / second; residents; $\beta = 2.64$ meter / second, $\chi^2 = 149.7, p < 0.001$). Also flying costs of migrants were higher ($F$)(migrants; $\beta = 98.7 \pm 7.6$, residents; $\beta = 69.6 \pm 9.2$ kJ per day, $\chi^2 = 10.0, p = 0.002$) as they spent more time flying (migrants; $\beta = 15.7 \pm 1.1$, residents; $\beta = 12.3 \pm 1.5$ minutes flight per day; $\chi^2 = 5.2, p = 0.023$). As a result, migratory geese experienced higher total energy costs ($TE$)(migrants; $\beta = 912.4$ kJ per day; residents; $\beta = 876.6$ kJ per day, $\chi^2 = 14.3, p < 0.001$, Figure 6.3c, d).

![Figure 6.3](image_url)

**Figure 6.3**: (A; B): Total grazing hours during the spring season for barnacle geese in the migratory (A) and the resident (B) population, by individual birds (thin lines) and the population average (thick lines). The dark green line shows the model regression over time, with total grazing time increasing from 14 February (migrants) or 12 February (residents). (C; D): Daily thermoregulation and total energetic costs during the spring season for migratory (C) and resident barnacle geese (D). The thin red line and area show thermoregulation costs, the thin black line shows total energetic costs, and the grey area shows the activity costs which contribute to the total energetic costs. The thick red and black lines show the model regression over time.
Onset of fuelling in resident and migratory populations

Birds can deposit fuel when their energy intake exceeds their energy expenditure (Lindström 2003), which can take place when their energy intake increase or their energy costs decrease. We find that barnacle geese of both populations started increasing their grazing time at February 14th (Figure 6.3a, b). During the fuelling period geese increased their grazing time with increasing daylight, both populations at the same rate ($\beta = 45.6 \pm 1.6$ minute increased grazing per hour of day length, $\chi^2 = 742.5, p < 0.001$; Figure 6.2c, d). Total energy expenditure ($TE$) started to decrease from February 5th (migrants) and January 25th (residents; Figure 6.3c, d). During the fuelling period total energy costs decreased at equal rates for both populations ($\beta = 1.46 \pm 0.13$ kJ decrease per day, $\chi^2 = 35.0, p < 0.001$). Thermoregulation costs ($T$) followed a similar trend ($\beta = 1.52 \pm 0.06$ kJ decrease per day, $\chi^2 = 26.8, p < 0.001$).

Discussion

Geese adjusted their grazing time to available foraging time during the day and the night, and mostly in winter also adjusted their grazing time to their energy expenditure. From mid-February onwards geese increased daytime grazing time during longer days, and their thermoregulation costs decreased, pinpointing the onset of fuelling. In contrast to our hypothesis, this onset of fuelling does not seem to differ between migratory and resident populations of barnacle geese. In the discussion we further explore whether geese have leeway to advance the onset of fuelling, and how this may explain the lack of difference between migratory and resident geese in the onset of fuelling.

Available foraging time

Grazing time of barnacle geese was strongly regulated by the time available for foraging. During the day, barnacle geese grazed for a stable fraction (residents 61%, migrants 66%) of the daylight hours throughout the season. Barnacle geese are known to be mostly diurnal foragers and during daylight hours spend around 80% of their time feeding (Ebbing et al. 1975; Prop & Vulink 1992). This is higher than our results on grazing time, but our measure differs from the definition of foraging used in observational studies, which also includes short bouts of food searching without actual pecking at forage plants (Sedinger & Raveling 1988). The fraction of daylight hours during which barnacle geese graze remains remarkably constant as the season progresses, suggesting that geese can only feed during a proportion of daylight hours. The remainder of the time they may have to spend time on other important activities, such as commuting to the feeding grounds, preening and washing, and being vigilant for predators (Metcalfe & Furness 1984). Geese may also be constrained by their digestive capacities (Sedinger & Raveling 1988; Kersten & Visser 1996), but this is unlikely to be the case in early spring, when foraging intake
and food retention times rates are low (Prop & Vulink 1992), and harvesting rate is likely a more important constraint (McWilliams & Raveling 1998). A digestive constraint may become important later in the season.

During the night, geese grazed more during moonlit hours. When necessary, geese are known to supplement daytime foraging by foraging at night (Owen 1972; Ebbinge et al. 1975; Riddington et al. 1996), which can add substantially to their daily intake (Tinkler et al. 2009). We find that early in the season, some geese relied for up to 50% of their daily intake on night-time foraging. Geese seem only able to graze in bright moonlit nights (Ebbinge et al. 1975; McWilliams & Raveling 1998). Night-time grazing occurred mostly early in the season, when short day length reduced foraging time during the day. In this way, barnacle geese kept to a constant daily foraging time of around 7 hours per day during winter months (January and February).

In addition to available time, geese also adjusted grazing time to their habitat. In natural salt and freshwater marshes, where food quality in terms of energy intake is slightly lower than in agricultural habitats (Prop & Black 1998; Eichhorn et al. 2012), geese increased their grazing time, likely in response to the lower food quality.

**Energy expenditure**

Geese increased their total grazing time when daily thermoregulation costs were higher, which may be an adaptation to match energy intake with energetic costs. This is also shown by the fact that migratory geese, which face higher energy costs in winter, seem to compensate for this by increased grazing time. At least during winter months, geese may aim to match their energy intake with their expenditure. As low temperatures in winter cause an increased energy expenditure (Ladin et al. 2011; Clausen et al. 2015) and time for foraging during daylight is short, geese are thought to be time-constrained to reach a sufficient energy intake to compensate for their energy expenditure (Owen et al. 1992; Tinkler et al. 2009), and as a result they often suffer from a loss in body mass (Ebbinge 1989; Tinkler et al. 2009; Ladin et al. 2011; Clausen et al. 2015). In order to explore this, we modelled the energy budgets of barnacle geese from time budgets, potential energy intake and energy expenditure (see supplementary material for methods). From the body mass trajectories of both populations it becomes clear that during winter months birds are close to energetic balance as they keep a constant body mass, or slightly decrease in body mass (Figure 6.4).

**The onset of fuelling**

From mid-February onwards, longer days enable geese to graze more than 7 hours per day by daytime grazing only, after which geese continue to increase grazing time with increasing day length. At the same time, their energy expenditure starts to decrease from early February onwards. From this moment onwards, the energy intake is likely to
exceed the expenditure (Lindström 2003), pinpointing the onset of fuelling. While this onset appears to be similar for migratory and resident population based on the onset of increase in grazing time and decrease in energy costs, we can closer examine this in the energy budget model. This model allows us to specifically evaluate the difference between intake and expenditure, and shows the moment of potential body mass increase. While we hypothesized resident geese to have advanced fuelling in response to an advance in laying dates, the modelled body mass trajectories (Figure 6.4) shows that populations do not differ in the onset of fuelling around early – mid March. However, resident geese seem to fuel faster in April, reaching an average body mass of 2300 grams earlier than their migratory counterparts. As resident geese never spend more time grazing than migratory geese, this appears to result from 1) a higher body condition after the winter period, during which resident geese can stay in energetic balance, and 2) a lower energy expenditure in spring, allowing for higher net energy intake.

![Figure 6.4: Modelled body mass trajectories over the season for individual birds (thin lines) and the population average (bold lines) for the migratory (light grey) and the resident (dark grey) population.](image)

**Advancing the onset of fuelling**

Geese will attain a higher fuelling rate when experiencing lower energy expenditure, which allows resident geese to gain a high body condition at an earlier date. This would be one way to advance fuelling, but geese may at the same time be able to advance the onset of fuelling. The onset of fuelling is determined by the moment when energy intake exceeds energy expenditure, and seems mostly driven by the increase in grazing time following more daylight hours in early spring. While this suggests that geese are limited in time available for grazing to advance the onset of fuelling, we also show that geese can supplement daytime grazing with night-time grazing, and are able to increase total
grazing time when facing high energetic demands. By these mechanisms geese could in theory reach a higher total grazing time early in the season than they currently reach, which would allow them to advance the onset of fuelling (Lameris et al. 2017c), as they would reach the tipping point where energy intake exceeds expenditure earlier in the season. This suggests that migratory and resident geese are not constrained in time to advance the onset of fuelling, as appears to be the case also for other herbivore species (Jeschke & Tollrian 2005). Grazing time still seems closely linked to day length, as both migratory and resident geese similarly adjust grazing time to day length. Given the lack of a time constrain, day length may not be an environmental constraint, but rather a cue to which the geese respond. Resident populations of barnacle geese may still use the same cues for the onset of fuelling as their migratory counterparts, while this has in fact become outdated in relation to their advanced reproductive season. An advancement of the onset of fuelling in the resident population may be restricted by the sensitivity of geese to increasing day length as a cue to increase grazing time.

Conclusions
When geese have to advance timing of migration under a warming climate, time available for foraging does not seem to form a limiting factor for an advancement in the onset of fuelling (Lameris et al. 2017c). This is especially true given the fact that barnacle geese, like many species of waterfowl, have in the past decades started utilizing agricultural landscapes for grazing, where quality of forage plants is greatly enhanced by addition of chemical fertilizers (van Eerden et al. 2005). Where barnacle geese previously switched to natural habitats as soon as these match the quality of agricultural areas (Prins & Ydenberg 1985), we have recorded at least some individuals which currently stick to utilizing agricultural habitats during spring staging (see also Box C). Although uptake of proteins is potentially lower in agricultural landscapes, intake rates of fat are much higher (Prop & Black 1998; Prop & Spaans 2004; Eichhorn et al. 2012), even early in the season. In line with the outcomes of a recent modelling study, advancement of fuelling and departure for migration under future climate warming may not so much be constrained by the time available for foraging or food availability, but rather by the lack of cues which correctly predict the optimal timing of migration (Lameris et al. 2017c). By the prerequisite of having acquired enough body stores before birds can depart for migration, an advancement of migration timing can be importantly limited by a lack of advancement of fuelling. As geese already seem unable to correctly predict, from their wintering grounds, the optimal timing of arrival on the breeding grounds (Kölzsch et al. 2015), adjustment of the onset of fuelling in line with rapid climate warming in the Arctic may not be possible.
Acknowledgements

We thank Cor van Aart, Peter Matthijssen, Peter de Vries and Morrison Pot for help during fieldwork in the Westplaat Buitengronden; Jaap and Gertrude de Leeuw for their hospitality and providing field support in the Westplaat Buitengronden; Gracie Adams and Morrison Pot for help during fieldwork on Schiermonnikoog; Götz Eichhorn, Jan van Walsem and Iris Chardon for help during laboratory work on the Netherlands Institute of Ecology (NIOO-KNAW); The department of Animal Ecology at the NIOO-KNAW and the Animal Movement Ecology group at the University of Amsterdam for fruitful discussion. UvA-BiTS studies are facilitated by infrastructures for E-Science, developed with the support of the Netherlands eScience Center (NLeSC) and LifeWatch, and conducted on the Dutch National E-Infrastructure with support from the SURF Foundation.
Supplementary material

1. Temperature variation between years

We compared temperature data for the wintering site of the migratory population (Northern Netherlands, weather station Lauwersoog) and the resident population (Delta region, weather station Hoek van Holland). Temperature data was downloaded from www.knmi.nl.

The daily average temperature (an average of both Lauwersoog and Hoek van Holland temperatures) follows a similar trend in 2015 and 2017 (Figure S6.1). Only 2017 temperatures in late March – early April and late May are higher than in 2015.

![Figure S6.1: Daily average temperature, averaged between weather stations Lauwersoog and Hoek van Holland, for 2015 (grey) and 2017 (black line).](image)

2. Deriving behaviours from accelerometer data

2.1 Training and validation dataset

We used this dataset to annotate the behavioural classes inactive, active and grazing. When a goose was sitting or standing still for a period longer than 1 s we annotated inactive behaviour. When a goose was walking (head up, not faster than 5 km/h for longer than 1 s) we annotated active behaviour. When a goose was foraging actively, with its head down and biting off grass tillers, for a period longer than 1 s, we annotated grazing behaviour. In all other cases (e.g. other behaviours or transition between behaviours) we did not annotate the data. We annotated the behavioural class of flying for accelerometer data collected during spring migratory flights of free-living geese, for which we annotated ‘flying’ when a goose was moving faster than 20 km/h and clear flapping acceleration in the z-axis were visible (Shamoun-Baranes et al. 2016).
2.2 Machine-learning model

To calibrate the machine learning model we randomly split the dataset of annotated behaviours (945 samples: 796 inactive, 57 active, 44 grazing, 48 flying) for training (0.4) and testing (0.6). The model was set up to use bouts of 10 accelerometer measurements. We selected features to use for the model by comparing model accuracy of a ‘pruned tree’ model for different combinations of features. Features retained in the final model were overall dynamic body acceleration, mean pitch (angle of the body along the z-axis), and mean absolute derivative of the acceleration of the x- and y-axis. We then ran a random forest model with 50 trees with the selected features. The final model correctly classified 0.99 of all behaviours ($N = 931$), ranging from 0.86 (grazing) to 1.00 (flying). This resulted in a Kappa statistic (a statistical measure to compare agreement between different annotations (Sim & Wright 2005) of 0.95. We then ran the machine learning model to annotate all accelerometer data associated with every GPS-fix in our dataset.

![Figure S6.2](image)

**Figure S6.2**: Time which geese spent grazing during the day relative to the day length (light grey) and during the night relative to night length (dark grey). Lines show linear regressions, data from the migratory population is shown in solid lines, data from the resident population is shown in dashed lines and darker shades.

3. Calculating flight costs

For each GPS-fix $i$, we determined the great circle distance in meters ($D_i$) between this GPS fix and the following GPS fix ($i + 1$). To determine when the bird had flown in between GPS fixes, we calculated the minimum groundspeed $V_{g min}$ (km/h) between these fixes as:

$$V_{g min} = \frac{D_i}{t_i} \quad (S6.1)$$
If $V_{g_{\text{min}}} > 0.28 \text{ m/s} (= 1 \text{ km/h})$, we considered that the bird had flown the distance between the two GPS-fixes. For these points we then calculated the total time of flight between fixes ($t_{\text{flight}}$) and the airspeed ($V_a$) of the bird:

\[ t_{\text{flight}} = \frac{D}{V_g} \]  

(S6.2)

\[ \sqrt{V_{a_i} = V_{g_{i}}^2 + V_{w_{i}}^2 - 2 \times V_{g_{i}} \times V_{w_{i}} \times \cos (\gamma - \omega)} \]  

(S6.3)

where $V_g$ is the ground speed, $V_w$ is the wind speed, $\gamma$ is the bearing of bird, $\omega$ is the wind direction. For $V_g$, we use the average groundspeed for all flight events for all individuals, which equals $14.68 \text{ m/s}$. As for every GPS-fix we now have duration and the time spent in flight, we correct the duration $t_i$ for the time spent in flight by subtracting $t_{\text{flight}}$ from $t_i$. The energetic costs for the remaining time period $t_i$ are calculated according to formula 1 (for behaviours grazing, active or inactive).

From the airspeed $V_{a_i}$, body mass $W_{i_{W_i}}$ and basal metabolic rate $BMR_i$ of the bird, we calculated the potential flight costs in kJ per minute $PF$ using the flight power theory developed by Pennycuick (Pennycuick 1989). We then calculated the actual flight costs $F_i$:

\[ F_i = PF_i \times t_{\text{flight}} \]  

(S6.4)

4. Energy budget model

4.1 General model

Energy budgets were calculated from 1) time budgets, 2) metabolisable energy intake from field data and 3) thermoregulation and existence energy. For one GPS-fix ($i$) every 30 minutes we calculated the bird’s body mass ($W_i$) as a result of body mass at the previous GPS-fix ($i - 1$) plus the net intake of metabolised energy ($I$) minus the total energy costs ($TE_i$), multiplied by the cost and efficiency of body mass storage or use. When energy is metabolised above the energetic needs, birds store the product ($P_i$) in the form of fat and protein stores with an efficiency of 0.8 (Blaxter 1989). When energetic costs exceed the metabolized energy, body stores are burned to gain energy with an efficiency of 1. Mass change, either for storing or burning body reserves, comes with a cost, for which we use the energy density of deposited tissues as calculated for female pink-footed geese, which equals 29 kJ/g (Madsen & Klaassen 2006).
Chapter 6

4.2 Metabolisable energy intake

4.2.1 Study sites
We calculated metabolisable energy intake from data on food quality and foraging intake rates collected in the wintering regions of migratory and resident geese. We conducted measurements on foraging plants, goose droppings and dropping rates of barnacle geese. We conducted measurements on a representative wintering site for migratory geese, the island of Schiermonnikoog in the Wadden Sea region (Eichhorn et al. 2012), from early March – mid-May 2016 in agricultural fields (n = 3 plots) and salt marshes (n = 3). For resident geese we collected data in agricultural fields (n = 3) and natural grasslands (n = 1) from mid-February to mid-April 2017 in the Delta region, with locations based on GPS-locations of tagged birds.

4.2.2 Field and lab methods
During measurements we collected fresh droppings and the upper leaves of the main forage plants for barnacle geese on Schiermonnikoog (van der Graaf 2006; van der Graaf et al. 2006) and the Delta (Uceda-Gomez unpublished data): Festuca rubra on Schiermonnikoog saltmarshes, Poa annua on Delta natural grassland and Lolium perenne on Schiermonnikoog and Delta agricultural fields. Forage plants were collected in temporal exclosures every 1 – 2 weeks, fresh droppings were collected in these same fields, after having observed defecating geese which had been present for at least 2 hours. We dried collected droppings and vegetation for 24 hours at 60°C. We weighed individual droppings to the nearest milligram after which samples were grind (Figure S6.3). We measured nitrogen concentration using a C:N analyser (Flash EA 1112 analyzer from Thermo Fisher Scientific Inc. Waltham, USA). We measured energetic value of samples (~ 0.5 g of dry material) using an IKA C5000 oxygen bomb calorimeter (Figure S6.3). We chemically determined the mass concentration of an indigestible marker (acid detergent fiber content, ADF, following Prop and Deerenberg 1991) using ANKOM Technology (Macedon, NY, USA) for a subset of samples. In order to comprise a model to estimate ADF from near-infrared (NIR) measurements, we took NIR measurements from all samples using a NIR spectrometer (Bruker MPA FT-NIR analyser with OPUS 7.0.129 software). From the chemical ADF measurements, and a larger set of samples (collected on vegetation and droppings from barnacle geese along their entire flyway between 2003 – 2015) we could successfully comprise a model which we used to estimate ADF for all samples. We determined the fraction of inorganic matter, and all chemical measurements were corrected to ash free dry matter basis (AFDM). We recorded the time between subsequent defecations of foraging geese (dropping rate $r$, analysed after Dokter et al. 2017) in March – mid-May on Schiermonnikoog and between April – June 2015 in the Delta region. We collected temperature data from the study site regions (from Lauwersoog for Schiermonnikoog and from Hoek van Holland for the Delta region, taken
from www.knmi.nl). From these data we calculated the growing degree days (GDD) with a base temperature of 0 °C (Lameris et al. 2017b).

4.2.3 Calculating metabolisable energy intake
Using sets of samples of forage plants and droppings which were collected at two week intervals we calculated the digestibility (Figure S6.3):

\[ D = 1 - \frac{ADF_g}{ADF_d} \] (S6.5)

where ADF<sub>d</sub> and ADF<sub>g</sub> is the acid detergent fiber content of droppings and grass respectively. Thereafter, we calculated the metabolizable energy intake \( R_{\text{metab}} \) by first determining the rate of excretory energy output \( (R_{\text{out}}) \) and ingested energy input \( (R_{\text{in}}) \) as:

\[ R_{\text{out}} = r * m_d * u_d \] (S6.6)

\[ R_{\text{in}} = R_{\text{out}} * \frac{ADF_d}{ADF_g} * \frac{u_g}{u_d} \] (S6.7)

where \( r \) is the dropping rate in droppings per minute, \( m_d \) the dropping weight, \( u_d \) and \( u_g \) the energetic content of droppings and grass respectively. For samples from Barents Sea region the energetic content was not measured and we used the average value of 18.6 kJ/g as this shows little variation between different species of plants (Prop & Black 1998). The rate of metabolised energy intake \( R_{\text{metab}} \) (kJ / min foraging) can then be calculated as:

\[ R_{\text{metab}} = R_{\text{in}} - R_{\text{out}} = q * R_{\text{in}} = \frac{q}{1-q} * R_{\text{out}} \] (S6.8)

where \( q \) is the apparent metabolisability, which equals:

\[ q = 1 - \frac{ADF_g}{ADF_d} * \frac{u_g}{u_d} \] (S6.9)

We then analysed the relationship between \( R_{\text{metab}} \) and growing degree days for both agricultural and salt marsh habitats (Figure S6.3). For every GPS-fix \( i \) we calculated the potential energy intake \( PI_i \) based on the habitat and growing degree day. To get a GDD for every GPS fox \( i \), we also calculated GDD for every day in the dataset of our tagged birds. We used temperature data from a range of weather stations in the Wadden Sea for the migratory populations (Lauwersoog, data from www.knmi.nl; Wangerland, Sankt-Peter and List, data from www.dwd.de) and from the weather station Hoek van Holland for the resident population (data from www.knmi.nl).
The actual metabolisable energy intake was then calculated as:

\[ I_i = P I * t_i \]  \hspace{1cm} (S6.10)

where \( t_i \) is the time interval from the GPS fix \( i \) until the following GPS fix \( i + 1 \).

4.3 Starting body mass

As we did not weigh the individual birds during staging at the wintering grounds, we derived a correlation between body size (measured as tarsus length * head length) and body mass from measurements of 29 female geese caught during winter 2008 – 2009 in the province of Friesland, the Netherlands (Ens et al. 2008). Using this correlation (body weight = 0.2186*(tarsus length * head length) + 254.43) we calculated body mass from tarsus length (as taken in summer 2014 at catch) for the 18 barnacle geese.

![Graphs showing digestiveibility, dropping mass, energy intake rate, and intake rate over months](image)

**Figure S6.3:** Digestibility and combustion energy content (ADFM corrected) in forage plants of barnacle geese, dropping mass and metabolisable energy intake on wintering and spring staging sites of migratory (orange) and resident geese (blue), for natural grasslands (dark orange, dark blue) and agricultural grasslands (light orange, light blue). Points show single measurements, lines show linear regression.
Table S6.1: Generalized linear mixed models for daytime grazing, night-time grazing, total grazing, time flight, flight costs, thermoregulation costs and total energy costs. Models include random effects of individually measured birds (ID). Coefficient values are given for fixed effects, and models are ordered from lowest to highest AICc values. Only models within 2.0 Δ AICc of the best model are shown.

### Daytime grazing (DTG)

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept</th>
<th>Population (P)</th>
<th>Day length (DL)</th>
<th>Habitat (H)</th>
<th>Interaction (P*DL)</th>
<th>degrees of freedom</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>Δ AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>DTG ~ P + DL + H + P*DL + (ID)</td>
<td>-6.294</td>
<td>16.03</td>
<td>-0.65</td>
<td>6.13</td>
<td>-4.79</td>
<td>7</td>
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<td>53281</td>
<td>0</td>
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### Night-time grazing (NTG)

<table>
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<th>Model</th>
<th>Intercept</th>
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<th>Habitat (H)</th>
<th>Date (D)</th>
<th>Date^2 (D2)</th>
<th>Moontime (MT)</th>
<th>Interaction (D*P)</th>
<th>Interaction (D2*P)</th>
<th>degrees of freedom</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>Δ AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>NTG ~ P + H + D + D2 + MT + P<em>D + P</em>D2 + (ID)</td>
<td>116.2</td>
<td>-43.14</td>
<td>-25.77</td>
<td>-2.612</td>
<td>0.0153</td>
<td>4.017</td>
<td>1.064</td>
<td>-0.003859</td>
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<tr>
<td>NTG ~ P + H + D + D2 + MT + P*D + (ID)</td>
<td>113.5</td>
<td>-33.36</td>
<td>-26.91</td>
<td>-2.504</td>
<td>0.0145</td>
<td>4.035</td>
<td>0.5918</td>
<td></td>
<td></td>
<td>-24639.51</td>
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### Total grazing (TG) pre-fuelling

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept</th>
<th>Population (P)</th>
<th>Date (D)</th>
<th>Interaction (D*P)</th>
<th>degrees of freedom</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>Δ AICc</th>
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<tbody>
<tr>
<td>TG ~ P + D + P*D + (ID)</td>
<td>471.3</td>
<td>-74.22</td>
<td>-1.444</td>
<td>0.896</td>
<td>6</td>
<td>-9428.818</td>
<td>18869.7</td>
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<td>TG ~ P + D + (ID)</td>
<td>463.9</td>
<td>-53.22</td>
<td>-1.131</td>
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<td>5</td>
<td>-9430.208</td>
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### Total grazing (TG) fuelling

<table>
<thead>
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<th>Model</th>
<th>Intercept</th>
<th>Population (P)</th>
<th>Date (D)</th>
<th>Interaction (D*P)</th>
<th>degrees of freedom</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>Δ AICc</th>
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<tbody>
<tr>
<td>TG ~ P + D + (ID)</td>
<td>-41.11</td>
<td>-13.553</td>
<td>45.62</td>
<td>5</td>
<td>16987.5</td>
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<td>TG ~ P + D + P*D + (ID)</td>
<td>-32.53</td>
<td>-98.29</td>
<td>44.96</td>
<td>6</td>
<td>16986.62</td>
<td>33985.3</td>
<td>0.24</td>
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<tr>
<td>TG ~ D + (ID)</td>
<td>-54.57</td>
<td>46.46</td>
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<td>4</td>
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<td>33986.8</td>
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#### Total grazing (TG)

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<th>Intercept</th>
<th>Population (P)</th>
<th>Day length (DL)</th>
<th>Moontime (MT)</th>
<th>Thermoregulation costs (T)</th>
<th>degrees of freedom</th>
<th>Log likelihood</th>
<th>AIC$_c$</th>
<th>$\Delta$AIC$_c$</th>
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<tbody>
<tr>
<td>Total grazing (TG)</td>
<td>-15.03</td>
<td>-46.28</td>
<td>36.48</td>
<td>5.266</td>
<td>0.09497</td>
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#### Total grazing (TG)

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<th>Intercept</th>
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<th>Day length (DL)</th>
<th>Moontime (MT)</th>
<th>Total energy costs (TC)</th>
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<th>AIC$_c$</th>
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#### Time flight (TF) pre-fuelling

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<th>Intercept</th>
<th>Population (P)</th>
<th>Date (D)</th>
<th>Interaction (D*P)</th>
<th>degrees of freedom</th>
<th>Log likelihood</th>
<th>AIC$_c$</th>
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</thead>
<tbody>
<tr>
<td>Time flight (TF)</td>
<td>9.281</td>
<td>3.019</td>
<td>0.3332</td>
<td>-0.33</td>
<td>6</td>
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#### Flight costs (F) pre-fuelling

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<th>Population (P)</th>
<th>Date (D)</th>
<th>Interaction (D*P)</th>
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<tr>
<td>Flight costs (F)</td>
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<td>1.616</td>
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<td>14878</td>
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#### Total energy costs (TC) pre-fuelling

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<th>Intercept</th>
<th>Population (P)</th>
<th>Date (D)</th>
<th>Interaction (D*P)</th>
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<th>Log likelihood</th>
<th>AIC$_c$</th>
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<td>Total energy costs (TC)</td>
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<td>2.004</td>
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<td>-7431.239</td>
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Table S6.1: Continued

### Total energy costs (TC) pre-fuelling

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<th>Date (D)</th>
<th>Interaction (D*P)</th>
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<th>Log likelihood</th>
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<tr>
<td>TC ~ P + D + P*D + (ID)</td>
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<td>-1.331</td>
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### Thermoregulation costs (T) pre-fuelling

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<th>Population (P)</th>
<th>Date (D)</th>
<th>Interaction (D*P)</th>
<th>degrees of freedom</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>Δ AICc</th>
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<tbody>
<tr>
<td>T ~ P + D + P*D + (ID)</td>
<td>825</td>
<td>12.7705</td>
<td>0.5486</td>
<td>-1.2773</td>
<td>6</td>
<td>-6504.29</td>
<td>13020.7</td>
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</tbody>
</table>

### Thermoregulation costs (T) fuelling

<table>
<thead>
<tr>
<th>Intercept</th>
<th>Population (P)</th>
<th>Date (D)</th>
<th>Interaction (D*P)</th>
<th>degrees of freedom</th>
<th>Log likelihood</th>
<th>AICc</th>
<th>Δ AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>T ~ P + D + (ID)</td>
<td>900.7</td>
<td>-17.13</td>
<td>-1.524</td>
<td>5</td>
<td>-15867.23</td>
<td>31744.5</td>
<td>0</td>
</tr>
<tr>
<td>T ~ P + D + P*D + (ID)</td>
<td>899.3</td>
<td>-12.737</td>
<td>-1.505</td>
<td>-0.055</td>
<td>6</td>
<td>-15867.13</td>
<td>31746.3</td>
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