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Optimal timing of migratory geese breeding in a warming Arctic

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BOX C

Habitat switch in a migrating herbivore: individual variation in switching behaviour of pre-migratory Barnacle Geese

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ABSTRACT

Arctic breeding birds, wintering in temperate regions, require large energy deposits in the form of fat as fuel for migratory flight, while some larger species, such as geese and swans, also bring energy deposits to the breeding grounds for reproduction. To attain sufficient energy stores, migratory birds require high daily intake rates of high quality food. During the period of extreme energy demand, it is common behaviour for animals to follow changes in nutritious food values by switching to a more profitable habitat or diet. Herbivores are not limited by absolute food abundances, but rather by food quality (digestibility). Pre-migratory barnacle geese along the Dutch Wadden Sea coast are known to switch from agricultural pasturelands to natural salt marshes in the course of spring. Using GPS-loggers to track movements of barnacle geese during spring, we show large individual variation in switching behaviour. To study which factors drive the seasonal habitat switch of geese, we combine data on GPS-positions, time-budgets and food quality, and assess how habitat choice affects disturbance events, grazing time and food intake rates. Individual geese switching to salt marsh habitat grazed for longer time periods and experienced less disturbance events compared to non-switching individuals. Individuals that did not switch and continued grazing in agricultural pasturelands gained higher fat deposition and a lower protein deposition than geese grazing in salt marshes. Net energy intake did not differ between switching and not-switching individuals, probably as higher energy intake of not-switching individuals was balanced by higher flight costs. Our results suggest that barnacle geese trade-off fast intake rates and high costs on agricultural pasturelands with slower intake rates and low costs on salt marshes, on an individual level.

Introduction

Many birds, especially those breeding in the arctic, undertake long-distance migrations between their wintering areas and breeding grounds. During migration most bird species rely on internal energy stores since they are unable to forage while flying. To fuel energetically costly migration flights, birds store energy in the form of fat before migration or at stopover sites (Lindström 1991; Bairlein 2001). Larger birds, such as geese and swans, also bring body stores to the breeding grounds for reproduction (capital breeding), because time constraints forces them to arrive in front of the peak in food availability (Meijer & Drent 1999; van der Graaf et al. 2006; Drent et al. 2007; Kölzsch et al. 2015). Pre-migratory fattening can cause dramatic changes in body mass. During this period, individuals can almost double their body mass in a couple weeks time in some wader species (Lindström & Piersma 1993). This is less dramatic for larger geese, as they experience slower fuelling rates (Klaassen 2003). Maximum fat deposition rates recorded are 10-15% of lean body mass per day (Bairlein 1990, 2001; Lindström 1991). Obviously, carrying this extra weight has costs, and fat deposition should occur fast and shortly before migration (Lindström 1991). To deposit sufficient energy and nutrient stores migrants require high daily intake rates of high quality food in preparation for their migration (Ebbinge et al. 1975; Drent & Prins 1987; Prop & Vulink 1992; Bairlein 2001).

Switching habitat and/or diet is common behaviour, especially in birds preparing for migration. To accumulate energy stores, pre-migratory birds follow changes in nutritive food value to be able to utilize high food abundances or high food quality. Habitat switches are common in waterfowl in which switching behaviour is often driven by food depletion (McWilliams & Karasov 2001; Nolet et al. 2002), waders that switch from shellfish during winter to arthropods during the breeding season in the arctic (Dekinga et al. 2001), while songbirds switch from insects to ample available fruits in autumn (Bairlein 2001). Most herbivores are however not limited by absolute food abundances, but rather by food quality, which is determined by protein content and digestibility of food plants. An example from mammalian herbivores is the blue wildebeest *Connochaetes taurinus*, which migrate away from grasslands with high resource availability to areas with more readily digestible food plants (Fryxell & Sinclair 1988). Especially avian herbivores with their limited guts rely on relatively high quality food. Winter staging Barnacle Geese *Branta leucopsis* switch from agricultural pastures to more natural habitats prior to migration to the Arctic (Prins & Ydenberg 1985; Prop & Black 1998). According to Prins & Ydenberg (1985) protein levels drop over the season, and switching occurs when protein levels in both habitats become equal. This would suggest that geese prefer the salt marsh, probably because lower levels of disturbance allow the geese to graze at a lower rate whereby digestion of carbohydrates is improved. A similar pattern is observed in pink-footed geese *Anser brachyrhynchus* switching from foraging in pasturelands to newly sown barley fields in spring (Madsen

1985), and Bewick's swans *Cygnus bewickii* switching from feeding on pondweeds to foraging on beet fields (Nolet et al. 2002).

Many geese populations have increased over the last 50 years, probably as a result of reduced human persecution, milder winters (Ebbinge 1991) and enhanced food supply due to investments in agricultural intensification (Fox et al. 2010). Geese and other herbivorous waterfowl have increasingly switched in land use during winter staging from natural habitats to nutrient rich agricultural habitats (van Eerden et al. 2005). Geese have become more dependent on agricultural crops as a food source during winter staging (Abraham et al. 2005; Fox et al. 2005; Eichhorn et al. 2012), to which they cause economic damage (Eichhorn et al. 2012; Nolet et al. 2016). Agricultural crops, especially grains and maize, are easy digestible and provide geese with high energy intake. It has been suggested that agricultural crops may not provide geese with sufficient protein deposition, whereas natural habitats, such as salt marshes, would provide geese with the necessary nutrients (Prop & Black 1998; Prop & Spaans 2004; Eichhorn et al. 2012). However, Eichhorn et al. (2012) found no differences in overall content and composition of amino acids between geese using either pastures or salt marshes, suggesting no impaired protein deposition in geese primarily using anthropocentric food sources. It is paradoxical that geese increasingly use anthropological food sources, where they are likely to experience more disturbance (Nolet et al. 2016).

With this study we aim to assess which factors drive the seasonal habitat switch of individual barnacle geese during spring staging. We hypothesize that geese behave optimally, resulting in a choice of habitat where they can maximize energy gain and minimize energy loss. We expect that energy gain is primarily determined by the availability of high amounts of high quality food, while we expect energy loss to be determined by flight movements and general metabolism (Nolet et al. 2016).

Methods

GPS data

In the summer of 2014 in the breeding colony of the Pechora Delta, Russia (68°40'N, 52°17'E), 40 female Barnacle Geese were captured on their nests using a spring-trap. UvA-BiTS GPS-loggers (19 g; Bouten et al. 2013) were attached to the geese with Teflon backpack harnesses (Lameris et al. 2017a). Full methods on the attachment of tracking devices can be found in Chapter 4. Data of 23 GPS-loggers was remotely downloaded in the summer of 2015. The GPS-loggers stored 48 GPS-locations per day and recorded 10 tri-axial accelerometer measurements (0.5 sec) at 20 Herz after every GPS-fix. Tri-axial accelerometers can measure posture, speed and body movements (Wilson et al. 2008; Halsey & White 2010) from which behavioural classes can be derived (Shamoun-Baranes et al. 2012).

Behaviour and time budgets

To classify behaviour of individual geese we calibrated a machine learning model which we trained and validated with a dataset of filmed behaviours from 8 captive barnacle geese. With this data we annotated the behavioural classes inactive, active and grazing. Inactive behaviour (n= 796) was annotated when a goose was sitting or standing still for a period longer than 1 sec. Active behaviour (n= 57) was annotated when a goose was walking faster than 5 km/h for longer than 1 sec with its head up. Grazing behaviour (n= 44) was annotated when a goose foraged actively, with its head down and biting off grass tillers, for a period longer than 1 sec. Flying behaviour (n= 48) was annotated using data of accelerometer data from spring migratory flights of free-living geese and was annotated when a goose was moving faster than 20 km/h and clear slopes of y acceleration were visible. Running, flapping with wings, preening or drinking was annotated as other behaviour. Remaining behaviours or transitions from one behaviour to another were not annotated. The dataset of annotated behaviours was randomly split for training (0.4) and testing (0.6) of the machine learning model. In the final model 98.5% of all behaviours was classified correctly. We used this final model to annotate all accelerometer data associated with the GPS-fixes in our dataset and to determine the time budgets of every individual barnacle goose. Time budgets were measured as the time between two data points, from which the behaviour registered at the first data point was chosen as a representative of the behaviour between the two points.

Habitat use and moment of switch

Habitat use in the Wadden Sea coast was measured as min/day in which a goose was grazing on either agricultural grasslands or natural habitats (salt marsh and fresh water marshes; Figure C.1). To determine the habitat use, we used the CORINE database to classify land use (Büttner et al. 2004; Büttner & Kosztra 2007). We determined land use for every GPS location where a goose was grazing, and distinguished between the land use classes salt marsh, freshwater marshes and agricultural grassland. For some fixes where a bird was indicated as grazing, we encountered other classes of land use. With 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. The geese were expected to make a habitat switch from pastureland to salt marsh in the course of spring. We determined this moment of switch for each individual as the date from which it spent $\geq 70\%$ of its foraging time on salt marsh habitat. Thirteen individuals showed a clear habitat switch (switching individuals), while 10 did not (not switching individuals; Figure C.2). In our analyses we therefore divided the geese in three groups: geese that do not switch

(group 1), geese that switch but graze in the period of the analysis on agricultural lands (group 2) and geese that switch but graze in the period of the analysis on salt marshes (group 3). The individual moment of switch ranged from julian date 53-126 (Figure C.2). We included time in our analysis by dividing the data in three periods: julian date 16-82 (period 1), julian date 83-106 (period 2) and julian date 107-130 (period 3).



Figure C.1: Map showing locations of barnacle geese from winter (January) until departure for migration (mid-May). Orange areas indicate locations in agricultural pastures and blue areas indicate natural (salt marsh) habitats.

Food availability

Greenness of the vegetation in grazing areas, measured by Normalized Difference Weight Index (NDVI), was used as a measure of food availability and plant nitrogen content (Walker et al. 1995; Ryan et al. 2012; Doiron et al. 2013). We measured the NDVI in the grazing areas using 16-day composite MODIS NDVI data (MOD13A2, glovis.usgs.gov) of the period between 2008 and 2010 which was collected by NASA's MODIS Terra satellite.

The data has a spatial resolution of 1 km and has been interpolated to obtain data with a temporal resolution of 1 day by a simple linear regression. We used these maps with the NDVI values per day to extract the values of the locations visited by geese while grazing in ArcMap (Version 10.1, 2012).

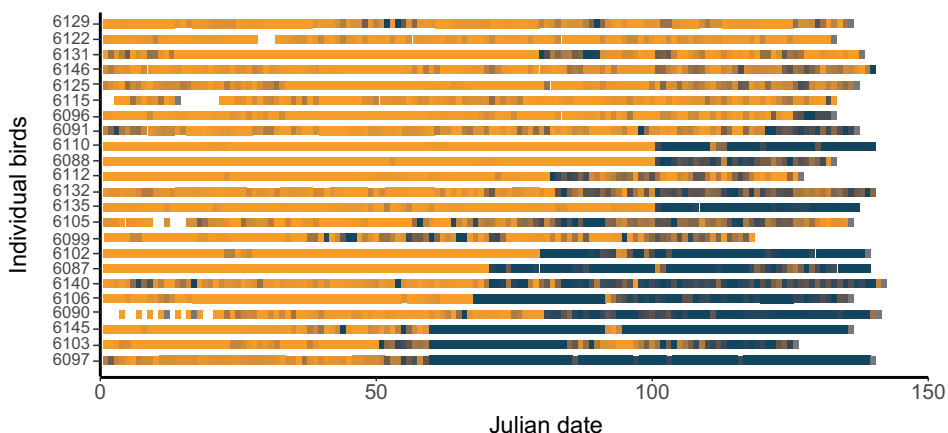


Figure C.2: Daily grazing locations of individual Barnacle Geese between 1 January until departure (mid-May). Orange bars indicate grazing on agricultural pastures, dark blue bars indicate grazing on salt marshes, and the intermediate colours indicate days when geese grazed both habitats.

Protein, fat and net energy intake

Data on intake rates was collected between March-May 2016 on the Dutch wadden island Schiermonnikoog (53°30'N, 6°10'E, see Prins & Ydenberg (1985) for detailed description of the study site). The island is a main wintering site for barnacle geese from the Russian breeding population. There are two habitats of interest to barnacle geese, agricultural dairy pastures in the western part of the island and natural salt marshes in the east. Sampling was done at 3 locations on agricultural pastureland where geese mainly forage on *Lolium perenne* and 3 locations on the salt marsh with *Festuca rubra* as main food plant.

Intake rates of fat (g), protein (g) and total energy intake (kJ) per day were calculated according to the methods used by Prop & Black (1998), for the period after the moment of switch. Dropping intervals, as a measure of defecation frequency, were obtained by observing an individual goose with a 30-60x telescope (Ebbinge et al. 1975, Prop & Black 1998). We only observed individuals that were grazing on an area for at least two hours, to be certain that vegetation of the current habitat was being passed through the digestive tract. Interval time (min) was measured using a stopwatch and dropping interval was analysed following (Dokter et al. 2017). After each observation, 10 fresh droppings were

collected and weighed and chemical analyses were done on their contents. In both habitats, 3 exclosures (0.5 m x 0.5 m x 0.5 m) were placed in representative subsections to prevent grazing by geese. Freshly grown vegetation from within the exclosures was collected every two weeks (using tweezers to imitate grazing), after which the exclosure was moved by 5 m in the same subsection. We calculated digestibility by measuring acid detergent fiber (ADF) in both food plants and droppings. We calculated ingestion rate (g/min^{-1}) by dividing the dropping rate by a measure of digestibility. Protein content of vegetation and droppings was derived from nitrogen content. Formulas used to calculate digestibility, ingestion rate of organic matter, digestion rate, retention efficiency of nitrogen, ingestion rate of nitrogen, retention rate of nitrogen, excretion rate of nitrogen, accumulation of nitrogen, accumulation of protein stores and accumulation of fat stores were calculated according to Prop & Black (1998).

Energy costs were determined as flight costs and basal metabolic rate (BMR). According to (van der Graaf et al. 2001) BMR of barnacle geese is 991 kJ/h. Flight costs were treated as $14 \times \text{BMR}$ (Riddington et al. 1996). Daily flight costs were multiplied by daily flight time in min to calculate daily flight costs.

Disturbance

Because geese fly away when disturbed (Nolet et al. 2016) we used distances that involved flight as a proxy for disturbance. When a goose moved a distance that is too long to be crossed without flying it was counted as a moment of disturbance. To differentiate between movements that could be crossed with and without flying we calculated the average speed in m/sec by dividing the distance covered during two GPS-fixes (calculated with the great circle distance formula) by the duration of the interval between the two fixes. For this average speed we established a threshold value of 0.1 m/sec by looking at different threshold values, from which it appeared that with a threshold value of 0.1 m/s or higher the same trends kept emerging, from which we assume that this threshold value was high enough to detect flights. Intervals in which geese on average moved more than 6 m/min were therefore labelled as flights, which we used as a proxy for moments of disturbance. We assume that we did not include roosting flights into our analysis, as roosting flights are known to occur before sunset and after sundown.

Statistical analyses

Linear models (LM) were used to assess statistical differences of daily grazing time, number of movements and NDVI values between switch groups with period included as a covariate. Generalized Linear Models (GLM), with foraging habitat as fixed factor and julian date as covariate, were used to assess the relation between nitrogen content of food plants and metabolizable energy with julian date for agricultural pasturelands and salt marshes. Intake rates were analysed using LM of daily fat deposition, protein deposition

and energy intake as a function of switch group with julian date as covariate. Additionally, we used Analysis of Variance (ANOVA) to assess for differences between switch groups. All statistical analyses were performed using R statistics (R Core Team 2017).

Results

Grazing time

Barnacle geese that did make a habitat switch increased their grazing time after they switched to the salt marsh, independently from the period in which the geese switched. Over the whole period, individuals grazing on the salt marsh spend more time grazing than the other two groups ($F_{5,1319}=136$, $p<0,001$). All geese increased their grazing time with julian date ($F_{5,1319}=136$, $p<0,001$, Figure C.3a).

Movements

Individuals that did not make a habitat switch, and thus stayed on the agricultural pasturelands, had higher daily movements than individuals that make a habitat switch to the salt marshes ($F_{5,1318}=86,92$, $p<0,001$). Individuals that did make a habitat switch made less movements on both the agricultural pasturelands and the salt marshes. All the groups differed in the amount of movements per period ($F_{5,1318}=86,92$, $p<0,001$, Figure C.3b).

NDVI

Switching individuals forage on agricultural pastures with the highest NDVI values before switching to the salt marshes ($F_{5,1319}=117,6$, $p<0,001$). Agricultural pasturelands visited by grazing geese have higher NDVI values than the salt marshes, which is in line with the field data on nitrogen content and digestibility ($F_{5,1319}=117,6$, $p<0,001$). In period 3, the NDVI values of places visited by the switching geese grazing on the salt marsh were significantly lower than in the other periods ($F_{5,1319}=117,6$, $p<0,001$, Figure C.3c).

Food availability

The nitrogen content in food plants of barnacle geese decreased with Julian date for both agricultural pasturelands (GLM, $n=19$, $t=-4.048$, $p<0.05$) and salt marshes (GLM, $n=18$, $t=-3.625$, $p<0.05$), but was in general higher for agricultural pasturelands (GLM, habitat: $F_{1,35}=35,049$, $p<0.001$, Julian date: $f_{1,35}=29.995$, $p<0.05$). Digestibility of food plants did not change with julian date on agricultural pasturelands (GLM, $n=9$, $t=-0.118$, $p>0.05$) and salt marshes (GLM, $n=7$, $t=0.183$, $p>0.05$). Digestibility of food plants from agricultural pasturelands was higher compared to food plants from the salt marshes (GLM, habitat: $F_{1,13}=5.804$, $p>0.05$, Julian date: $F_{1,13}=0.015$, $p>0.05$). The potential intake rates of metabolizable energy differed between the agricultural pasturelands and the salt marshes, the metabolizable intake rate was higher on agricultural land (GLM, location

$F_{1,34} = 10.139$, $p < 0.05$; Julian date $F_{1,34} = 5.715$, $p < 0.05$). Moreover, the intake rates on the agricultural lands increased over time (GLM, $n = 7$, $t = 2.890$, $p < 0.05$), whereas we found no such trend in the intake rates on the salt marshes (GLM, $n = 6$, $t = 1.282$, $p > 0.05$).

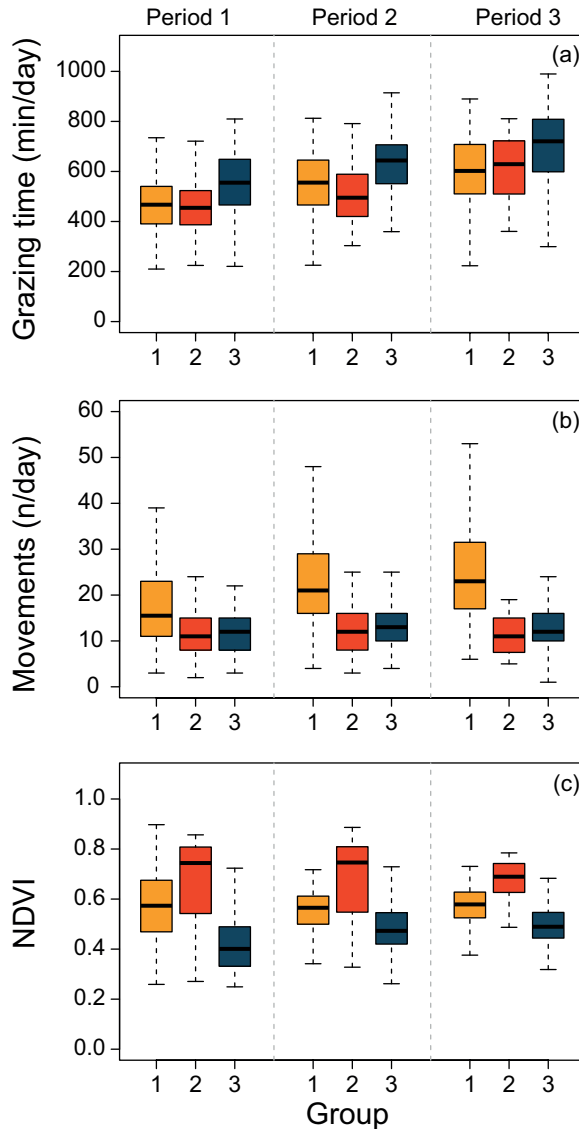


Figure C.3: Boxplots showing the distribution of daily grazing time in min (a), number of movements (b) and NDVI values (c) of Barnacle Geese divided in groups and periods. Groups are indicated as 1= not switching individuals (orange), 2= switching individuals still using agricultural pastures and 3= switching individuals grazing on salt marshes (dark blue). Periods 1-3 refer to Julian date 61-82, 83-106 and 107-130 respectively.

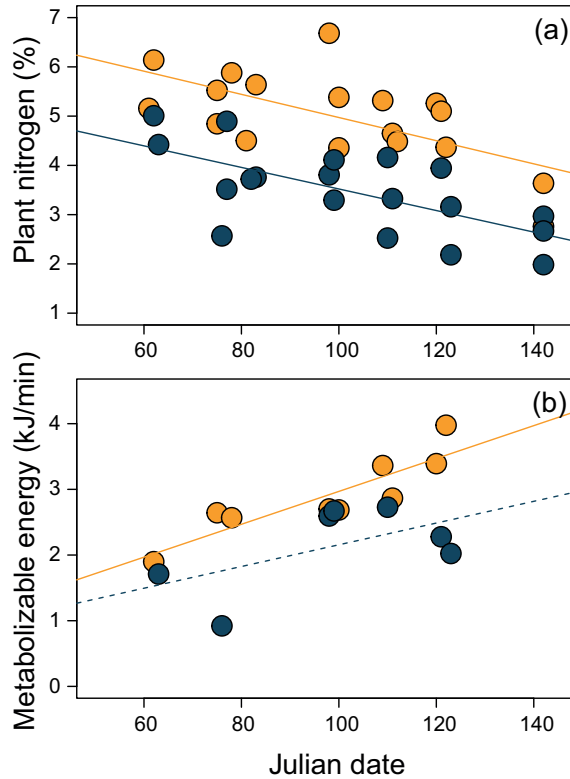


Figure C.4: Plant nitrogen content (%) for *Lolium perenne* (agricultural pasturelands) *Festuca rubra* (salt marshes) (a) and metabolizable energy intake (min) (b) with julian date on agricultural pastures (orange) and natural (salt marsh) habitat (dark blue).

Intake rates and energetic costs

Fat deposition differed significantly between switch groups (ANOVA, $df= 2$, $f= 204.6$, $p<0.001$). A post-hoc Tukey test showed that individuals in switch group 1 and 2 were not significantly different, whereas individuals in switch group 3 had significant lower fat deposition compared to those in switch group 1 and 2 ($p<0.001$, Figure 5a). Protein deposition was significantly different between switch groups (ANOVA, $df= 2$, $F= 40.33$, $p<0.001$). A post hoc Tukey test showed that individuals in switch group 1 and 2 were not significantly different, but individuals in switch group 3 had significant higher protein deposition than individuals in switch group 1 and 2 ($p<0.001$, Figure 5b). Flight costs were significantly different between switch groups (ANOVA, $df= 2$, $F= 3.519$, $p<0.05$). However, a post hoc Tukey test did not show significant differences between groups ($p>0.05$, Figure 5c). Net energy intake differed significantly between switch groups (ANOVA, $df= 2$, $F= 71.75$, $p<0.001$). A post hoc Tukey test showed that individuals in switch group 2 had significant lower energy intake compared to individuals in switch group 1 and 3 ($p<0.001$),

and that individuals in switch group 3 had significant higher energy intake than those in switch group 1 ($p < 0.001$, Figure 5d).

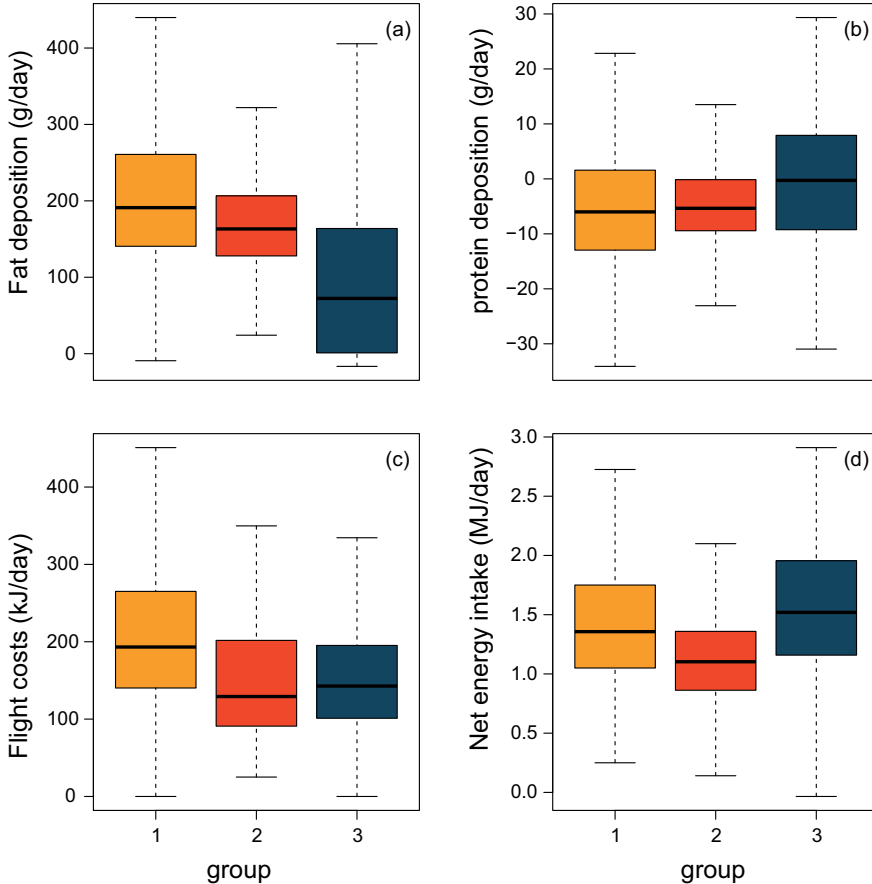


Figure C.5: Boxplots showing the distribution of daily fat deposition in g (a), protein deposition in g (b) and energy intake in MJ (c) of Barnacle Geese that do not make a habitat switch (group 1, orange), perform an early habitat switch (group 2, red) or perform a late habitat switch (group 3, dark blue).

Discussion

Our results provide evidence that pre-migratory Barnacle Geese staging at the Wadden Sea coast decide on an individual level whether to make a habitat switch, and if so, at what moment during spring this habitat switch is being made (ranging between Feb-May). Although geese experience higher potential energy intake in agricultural habitats, this appears to be a trade-off with higher energy costs due to increased disturbances and

higher flying costs. Individuals which switch to salt marsh habitats graze more in order to compensate for the lower food quality, but can reach equal net energy intake compared to geese that do not switch.

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