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Changes in Behaviour and Proxies of Physiology Suggest Individual Variation in the Building of Migratory Phenotypes in Preparation for Long-Distance Flights

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Long-distance migration in birds is a complex syndrome that involves high energy costs and, in some species, substantial physiological re-organisation. Such flexible migratory phenotypes are commonly associated with bird species flying non-stop across vast ecological barriers, where there are few opportunities to stop and refuel *en route*. Prior to making migratory flights, some species have been found to atrophy organs that are not required (e.g., digestive organs) and grow those associated with powering flight (pectora muscles and heart), presumably to optimise costs. However, most studies of this flexibility have required sacrificing study animals and this has limited our capacity to measure individual variation and its potential consequences. Here we investigate the behavioural and, indirectly, physiological adaptation of an arctic breeding long-distance migrant the light-bellied brent goose *Branta bernicla hrota*, during spring staging in southwest Iceland. We use a sequential sampling approach to record behavioural observations and conduct stable isotope analysis of faecal samples from uniquely marked individuals to assess protein catabolism. Individuals showed a three-phase fuel deposition process, with initial slow intake rates followed by hyperphagia and then a period of inactivity immediately prior to migratory departure (despite multiple days with favourable wind conditions). The C:N ratio and δ^{15}N values in faeces were significantly linked to fat deposition during the latter stages and suggests catabolism (reorganisation of proteins) occurring prior to departure. Our results suggest a strategic delay in migratory departure to enable reorganisation into a flying phenotype and that the extent of this varies among individuals.

Keywords: migratory birds, spring staging, phenotypic flexibility, atrophy, behaviour

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INTRODUCTION

Long-distance migration is a remarkable behaviour involving the cyclical movement of animals often directed by seasonal variability of global resources (Piersma et al., 1999; Saino et al., 2010; Soriano-Redondo et al., 2020). Despite the high energetic costs of travelling such long distances, it is a strategy that enables species to expand their range, exploiting specific habitat niches best suited to their current life history stage (Hedenström, 2008). Although widespread in the animal kingdom, it is commonly associated with bird species and often characterised by extensive non-stop flight over vast ecological barriers (Saino et al., 2010; Hou and Welch, 2016). This can be physiologically demanding as sparse opportunities for groundings cause extended periods of fasting while still maintaining high metabolic activity (Lindström and Piersma, 1993; Piersma and Gill, 1998; Bauchinger and Biebach, 2001; Bauchinger et al., 2005; Scott et al., 2015; Remisiewicz et al., 2016).

To deal with the high energetic costs of migration, birds often rely on staging sites along their migration route. These act as stepping stones where individuals can rest and refuel before resuming the journey (Mehlman et al., 2005). Staging and refuelling birds undergo significant physiological changes, switching between wholly catabolic states during flight to a largely anabolic state during stationary periods (Landys-Ciannelli et al., 2003). In an effort to efficiently replenish energy stores and gain substantial amounts of adipose fat, birds will enter a state of hyperphagia upon arrival at the staging site (Lindström, 2003). However, fat accumulation is not the only physiological change occurring during a stopover (Karasov and Pinshow, 1998; Battley et al., 2000; Gannes, 2002). The avian digestive system is known to be flexible with associated muscles and organs undergoing hypertrophy during hyperphagic feeding and atrophy during flight induced fasting (McWilliams and Karasov, 2001; McWilliams et al., 2004). Likewise, organs involved in maintaining high performance sustained migratory flights such as pectoral muscle and heart, undergo hypertrophy in the days prior to departure from the staging grounds (Marsh, 1984; Gaunt et al., 1990; Evans et al., 1992; Piersma, 1998; Piersma et al., 1999; Lindström et al., 2000; Bauchinger and Biebach, 2005; Dietz et al., 2007). Due to the excessive metabolic cost needed to maintain the digestive system and the energetic cost associated with carrying its weight, Piersma (1998) suggests that long-distance migrants with no immediate necessity for these organs gain an advantage in reducing them before embarking on a migratory flight. For example, bar-tailed godwits (*Limosa lapponica*), increase stomach mass by 30% during the first half of spring staging only to decrease its mass by 20% before migratory departure (Piersma and Lindström, 1997; Piersma and Gill, 1998). Jehl (1997) provides further evidence for this migratory strategy of phenotypic flexibility, finding eared grebes (*Podiceps nigricollis*) pre-departure reduce their stomach, liver and intestine by up to 57%.

The energetic constraints for avian migrants vary according to environmental conditions encountered *en route* and their life history strategies, the latter being particularly acute for large-bodied High Arctic breeders. Given the scarce foraging opportunities available on arrival at the breeding site, they are often capital breeders, relying on endogenous resources to initiate and finance breeding (Drent et al., 2007; Drent and Daan, 1980; Jaatinen et al., 2016). While Arctic migrants can benefit from 24-h daylight and abundant food resources over summer, this is restricted to a narrow period where conditions are optimal to successfully breed and fledge offspring (Poussart et al., 2000; Drent et al., 2007; Jónsson et al., 2009). Reproductive success is shown to significantly decline with a later laying date, however, eggs laid earlier in the season were found to be formed using a higher proportion of endogenous resources (Lepage et al., 2000; Bêty et al., 2004; Schmutz et al., 2006). This highlights the importance for High Arctic migrants to gain adequate resources at staging sites along the flyway, enabling a timely arrival and rapid initiation of breeding (Hupp et al., 2006; Schmutz et al., 2006).

A number of studies have highlighted the extent of phenotypic flexibility during spring migration in birds [e.g., *Red knot* (*Calidris canutus rogersi*): Battley and Piersma, 1997, (*canutus/islandica*) Piersma et al., 1993; *Great knot* (*Calidris tenuirostris*): Battley et al., 2000, *Eared Grebe*: Jehl, 1997, *Bar-tailed Godwit:* Piersma and Gill, 1998, *Dark-eyed junco* (*Junco hyemalis*): Ramenofsky et al., 1999, *Garden warbler* (*Sylvia borin*): Biebach, 1998; Bauchinger et al., 2005, *Greater snow goose* (*Anser caerulescens atlanticus*): Gauthier et al., 1984]. However, our understanding of this phenomenon has often come from a small number of sacrificed individuals, as shown in the above-mentioned studies, or from controlled feeding and simulated migration experiments (e.g., Karasov et al., 2004; Pierce and McWilliams, 2004). Research specifically interested in flight physiology, measuring changes in protein and lipid catabolism are able to use non-invasive sampling techniques *in situ* (e.g., *pigeons* (*Columba livia*)*:* Hatch et al., 2002, *Western sandpiper* (*Calidris mauri*): Guglielmo and Williams, 2003]. However, many of these studies remain cross sectional, only measuring an individual's physiological state once. These methodologies inhibit the study of within-individual level variation and the potential link to downstream fitness consequences (Piersma and Gill, 1998). Our study presents a route to overcoming difficulties in longitudinal sampling by using behavioural observations and stable isotope analyses of faecal deposits as proxies for large scale reorganisation of internal tissues. We sequentially sampled from marked light-bellied brent geese (*Branta bernicla hrota*) during their spring migration staging in southwest Iceland. While stable isotope measures: C:N ratio, $^{13}C/^{12}C$ ($\delta^{13}C$) and $^{15}N/^{14}N$ ($\delta^{15}N$) have been extensively used to characterise the diets of animals, they can also be used to infer physiological reorganisation (Hobson and Clark, 1992; Inger and Bearhop, 2008). Birds experiencing nutritional stress regardless of diet are known to mobilise and deposit proteins between bodily tissues resulting in additional isotopic discriminations and the enrichment of heavier nitrogen isotope in faeces (Hobson and Clark, 1992). By considering stable isotope analyses alongside food intake rate there is the potential to infer rates of protein catabolism in staging migratory birds. This in turn allows us to assess the extent to which individual animals exhibit phenotypic flexibility, through the reorganisation of body proteins in preparation for a period of migratory flight and subsequent fasting. The east Canadian High Arctic population of Light-bellied brent geese are an excellent model system for such a study. They are herbivorous capital breeding migrants, staging in west Iceland prior to a long-distance flight into the breeding grounds and there are a large number of individually marked birds in the population making it easy to follow individuals through time (Inger et al., 2010).

We predict that phenotypic flexibility will be evident in the light-bellied brent geese during their one staging event on spring migration, manifesting as (1) elevated foraging and locomotor activity soon after arrival, (2) increased δ^{15}N and decreased C:N ratio in feaces just prior to migratory departure, and (3) a period of reduced foraging and locomotor activity prior to departure irrespective of favourable wind conditions being present.

MATERIALS AND METHODS

Study System

We conducted our study in Álftanes (southwest Iceland, 64° 06′N, 22° 00′W), a main spring staging site for light-bellied brent geese of the East Canadian High Arctic population (ECHA). We carried this study out during the brent goose spring migration staging (01/05–27/05/2017), a critical period of intense foraging, where birds accumulate energy stores for migratory flight and breeding (Inger et al., 2008, 2010). In late April, the population has a staggered migration from wintering grounds along the Irish coasts to staging sites in west Iceland (Inger et al., 2008). They typically resume migration *en masse* approximately one month later to their breeding grounds in the Canadian High Arctic (Gudmundsson et al., 1995; Clausen et al., 2003; Robinson et al., 2004). The ECHA population amounts to approximately 35000 individuals of which over 10% are uniquely marked with coloured *Darvic* leg rings displaying individual alphanumeric combinations (Cleasby et al., 2017). We conducted this study on marked individuals only and all observations in this study were made from inside of a vehicle, through an Opticron HR 80 GA ED telescope with an SDLv2 40936 zoom eyepiece (×54 zoom) and Meopta Meo Star B1 12 × 50 HD binoculars, causing minimal disturbance to geese. We observed birds at opportunistically selected field sites around Álftanes from 6.00 h to 22.00 h.

The age of geese (juvenile/adult) was visually determined in the field by observation of plumage colouring along the edges of wing coverts, clearly distinguishing juveniles from adults (Reed, 1993). We identified relationships between individuals [partners/family with parent(s) and offspring/single adults/single juveniles] by observing proximity and cohesion during birds' movements, which was found to represent a reliable method of identifying first-order relatedness among individuals (Harrison et al., 2010). We recorded flock size and considered individuals at least 20 goose lengths apart as a different flock.

Abdominal Profile Index

We opportunistically re-sighted marked birds and recorded fat deposition on foraging geese by visually determining abdominal profile indices (API; Owen, 1981; Boyd et al., 1998; Clausen et al., 2003; Madsen and Klaassen, 2006) on a seven-point scale (1–7; 1 being lowest and 7 the highest score; Inger et al., 2008) with accuracy of 0.5. The API score is linearly related to body mass and highly correlated with the size of abdominal fat reserves (Fox et al., 1999; Madsen and Klaassen, 2006). It is commonly used on geese and shorebirds as they are known to predominantly store energy in their abdominal cavity (Owen, 1981; Wiersma and Piersma, 1995; Boyd, 2000; Tinkler et al., 2007). We used APIs as an indication of body condition and weight gain. We have evidence from this population and other closely related taxa that it correlates with body mass and subsequent reproductive success (Ebbinge and Spaans, 1995; Tinkler et al., 2007; Inger et al., 2008; Harrison et al., 2011; Harrison et al., 2013).

Peck and Pace Rate

We measured foraging behaviour of individual geese through focal sampling of peck and pace rates. Identifiable geese were initially randomly selected then resampled each week of the staging period. We classified pecks as movement of the beak toward the ground, thereby touching the substrate, and paces as every step taken by an individual (Inger et al., 2006a). We used tally counters to record the number of pecks and paces over 1–2 min and obtained a rate by dividing the number of pecks/paces by the total length of observation. We did not include observations in which birds simultaneously did not peck nor pace in this study. Additionally, we recorded length and occurrence of sitting behaviour when geese sat on the ground during a focal observation.

Stable Isotopes

We used faecal sample collection of marked geese for stable isotope analyses. Given brent geese feed on saltmarsh (marine) and terrestrial grasses, which are isotopically distinct with δ^{15}N values being lower in terrestrial grasses and δ^{13}C values being considerably higher in marine grasses, we classified all field sites accordingly accounting for the resulting difference in carbon and nitrogen stable isotope ratios in faecal samples (Inger et al., 2006b). For collection of faecal samples, we split the field season into three time periods: *early* (May 1–10) reflecting arrival and the onset of hyperphagia, *mid* (May 11–19) reflecting a full hyperphagia and *late* (May 20–27) reflecting the cessation of hyperphagia and preparation for migration. We chose these time periods in response to the feeding rate of geese measured across the spring, i.e., initial increase of feeding rates and API (onset of hyperphagia), reaching a peak toward the end of the staging season (full hyperphagia) and a subsequent drop of feeding rates and API until departure (cessation of hyperphagia). Such a mass trajectory and feeding rate pattern has also been recorded in other *Branta* populations during spring staging, for example in dark-bellied brent geese (*Branta bernicla bernicla*) on their last spring staging site before embarking on a long-distance flight to their Arctic breeding grounds (Dokter et al., 2018). In the *early* period, we collected samples from a range of identifiable individuals and then resampled from these target individuals in each subsequent time period, to track individual variation throughout staging. We collected faecal samples from known individuals with one person observing the targetted goose until it defecated and a second collecting the sample by following directions of the observer through two-way radios. Faecal samples were stored at −20°C in conventional plastic-zip lock bags until analyses.

We subsampled faecal samples along a central horizontal plane of the cylindrical pellet. We freeze-dried samples, ground them into a homogenous powder, and weighed them to 0.7 mg (±0.1 mg) in tin capsules. Stable carbon and nitrogen isotope measurements were determined by a Thermoquest EA1110 elemental analyser interfaced with a Europa Scientific 2020 isotope ratio mass spectrometer (Elemtex Ltd., Cornwall, United Kingdom). Stable isotope ratios were expressed as δ notation, measured in parts per thousand (‰) relative to international standards Pee Dee Belemnite for carbon and air for nitrogen according to the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio of $^{15}N/^{14}N$ or $^{13}C/^{12}C$. We report stable isotope ratios as $\delta^{13}C$ values for carbon and $\delta^{15}N$ values for nitrogen and data are corrected for sample mass and instrument drift. Measurement precision (standard deviation), based on within-run replicate measures of the laboratory standard, was better than 0.25‰ for $\delta^{15}N$ and 0.21‰ for $\delta^{13}C$ isotopic values.

Wind Conditions

Past studies have shown that long-distance migrants will time their departure to maximise wind support (Grönroos et al., 2012). Using the package "*RNCEP*" (Kemp et al., 2012) in R, we interpolated the 10m above ground U wind (east/west) and V wind (north/south) components (m/s) for a central point on the Álftanes peninsula (64° 06′N, 22° 00′W) using the NCEP/NCAR dataset (Kalnay et al., 1996), provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, United States[1]. Measurements were interpolated on the hour each day between 15 May (15 days prior to departure) and 5 June 2017 (5 days post departure) inclusive.

To model U and V wind as a function of wind support and crosswind we estimated the birds flight direction (heading) on migratory departure using the "*geosphere*" package (Hijmans et al., 2017). By studying the migratory tracks obtained from birds in this population, it is known that light bellied brent geese fly west north west toward Greenland, therefore a reference point on the southeast coast of Greenland was used to calculate heading (65° 42′N, 37° 42′W). Wind support and crosswind were calculated using methods described by Safi et al. (2013) (**Figure 1**). Positive values associated with wind support represented a tail wind and negative values a head wind. Crosswind was taken as an absolute value irrespective of direction (Safi et al., 2013).

Statistical Analyses

We conducted all data analyses using R software version 3.3.1. (R Core Team, 2016). We determined the sex of marked individuals as described in Bodey et al. (2020) by using a discriminant function based on morphological differences between wing length and head-bill of male and female individuals, recorded during catches when darvic rings are attached. All birds that did not fit male or female morphological criteria were classified as "unknown" and were excluded from statistical analyses.

Abdominal Profile Index

To determine the inflection point in observed API values in our dataset, we defined an *nls* function in the native *stats* package using API as a dependent variable and including date in May as an independent variable. For this function, we modelled date in May as sigmoid equation as the sigmoid curve best fit the distribution of API values and therefore allowed for an adequate estimation of the inflection point. We further used a linear plateau model to determine an approximate date during spring staging when weight gain of brent geese attenuated. We defined an *nls* function in the native *stats* package with date and API score as x and y variables along with three parameters aiming to define the best fit intercept, slope, and critical x value (Mangiafico, 2016). Once we determined the critical x value (=date when API started attenuating), we used linear models, fitted with the R package *lme4* (Bates et al., 2014), to test if API and date in May were correlated before API score attenuation and after API attenuation. We used API as a dependent variable and individual sex and date in May as independent variables. We did not add ID of geese as a random effect to the models as each individual only occurred once in the dataset.

Peck and Pace Rate

We used the *glmmTMB* R package (Magnusson et al., 2017) to design global generalised linear mixed models (GLMM) for peck and pace rates of individuals. We fitted both models with negative binomial errors and a log link function. The models had either peck or pace rate as the dependent variable and z transformed: Julian date, API, flock size (log transformed); whether the birds had a partner and/or juveniles, sex, and resource type (marine vs. terrestrial) as independent variables. We used z transformations for API, Julian date and flock size as their scales had a large amount of variation. Furthermore, we included the individual identification (leg ring combination) of each sampled goose as a random intercept term into the models as most geese were sampled multiple times throughout staging. We selected minimal adequate peck and pace rate models (MAMs) by using the *dredge* function of the R package *MuMIn* (Barton, 2009). The *dredge* function returns a list of all possible models with the given predictors, which we set to be ranked by second-order *Akaike information criterion* (AICc) values (Burnham and Anderson, 2004). For both (peck and pace) MAMs we chose the model with the lowest AICc value. To investigate changes in proportional occurrence of sitting behaviour in every week of staging, we used a repeated-measures ANOVA and Tukey's *post hoc* test with *Bonferroni* correction.

Stable Isotopes

To determine the effect of independent variables: API, date, resource type (marine vs. terrestrial) and sex on the dependent variables: C:N ratio, $^{13}C/^{12}C$ ($\delta^{13}C$) or $^{15}N/^{14}N$ ($\delta^{15}N$) values obtained from faecal samples, we fitted linear mixed models using the *lme4* R package (Bates et al., 2014). We added the individual goose ID as a random intercept term in the models. API was included as either the individuals recorded value (1–7) or categorised as below, above or at population average (group mean centring). We determined population average using the

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[1] http://www.esrl.noaa.gov/psd/

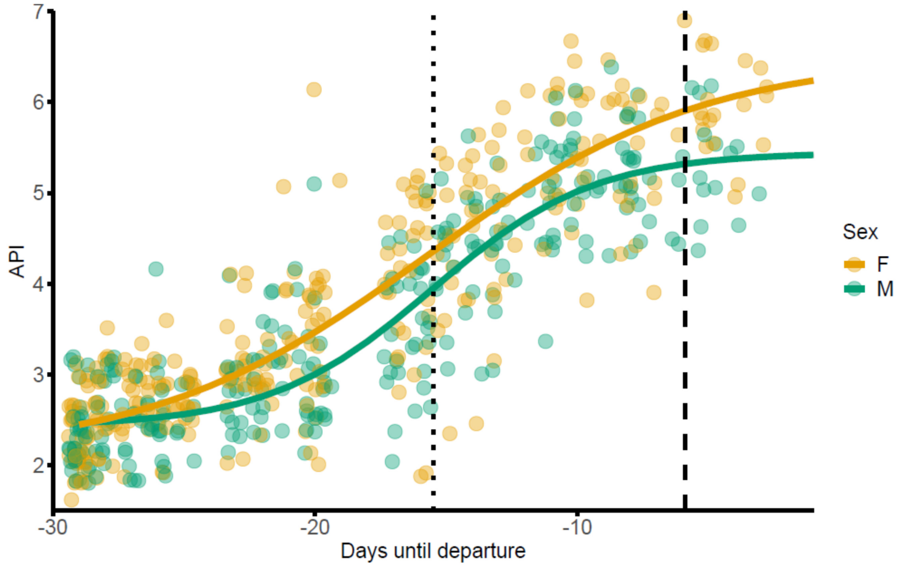

FIGURE 1 | Increase in body condition of brent geese during spring staging in Álftanes, Iceland, as measured by the abdominal profile index (API). Migration to breeding grounds was resumed *en masse* by brent geese on 30/05/17. Females are represented in orange and males in green. The dotted line is the point of inflection, when the rate of weight gain begins to slow (x = 14–15/05/17). The dashed line represents the trough in the second derivative of the sigmoidal function, when the rate of weight gain begins to attenuate (x = 24/05/17).

daily mean API values from re-sighting data collected throughout the staging period in Álftanes. We achieved MAMs by creating all possible models with the given predictors using the R *dredge* function and AICc comparisons. To determine the effects of date, habitat and sex on API (in the Stable isotope dataset), we fitted another linear mixed model with the given responses and individual goose ID as random effect. We used a Tukey's *post hoc* test to determine differences in δ^{15}N, δ^{13}C and C:N for above/below API individuals across the weeks of spring staging.

RESULTS

We recorded 1,185 re-sightings of 292 uniquely identifiable light-bellied brent geese between May 1–27, 2017 on 9 intertidal saltmarshes and 14 terrestrial field sites. Most birds arrived at study sites before the start of data collection (last days of April) but bird numbers continued to increase during the first week of our study. The bulk of the staging population departed *en masse* from the study area on May 30.

Abdominal Profile Index

The linear plateau model indicated that individuals in this study population reached a plateau in weight gain measured as an abdominal profile index (1–7), of approximately 6 between May 24 and 25 (n = 187 observations, 187 individuals, critical day value = 24.5, 95% CIs: 20.8–28.2, plateau y = 5.7, $p < 0.001$; **Figure 1**). Furthermore, a significant positive linear correlation between API and the number of days into staging was observed until May 24 (n = 172 observations, 172 individuals, $r^2 = 0.70$; est. = 0.15, SE = 0.01, $p < 0.001$) but no such correlation was observed thereafter (n = 13 observations, 13 individuals, $r^2 = 0.41$; est. = 0.05, SE = 0.22, $p = 0.81$). However, after May 24 female geese had higher API compared to males (n = 13 observations, 13 individuals, $r^2 = 0.41$; est. = 22120.96, SE = 0.33, $p = 0.02$). A sigmoid function modelling API by day shows both males and females experience the inflection point in weight gain 15.3 days prior to departure (n = 187 observations, 187 individuals; $r^2 = 0.80$, est. = 15.31, SE = 0.71, $p < 0.001$; **Figure 1**).

Peck and Pace Rate

The top ranking peck rate model, selected by lowest AICc value, included Julian date, the quadratic term of Julian date and resource type as independent variables (AICc = 1757.8, AICc null model = 1759.2; **Table 1**; model selection table in **Supplementary Material 1**). As might be expected given the trajectories, only the quadratic effect of Julian date had a statistically significant negative influence on peck rates during staging (n = 154 observations, 73 individuals, est. = −0.133, SE = 0.054, $p = 0.013$), meaning that peck rates of geese initially increased in the earlier part of the staging period and then decreased again at the end of staging (**Figure 2**).

The best performing pace rate MAM only included Julian date as an independent variable but only differed marginally from the null model (AICc = 1,357.2, AICc null model = 1,357.5; see **Supplementary Material 2** for AICc model selection table). Julian date did not influence pace rates statistically significantly (n = 154 observations, 73 individuals, est. = −0.089, SE = 0.058, $p = 0.121$). Yet, we observed that sitting behaviour differed statistically significantly between the four weeks of staging ($F_{1,3} = 6.727$, $p < 0.001$) and a Tukey *post hoc* test revealed that sitting behaviour was higher in the last week of staging compared

TABLE 1 | GLMM output with peck rate as dependent variable and food resource type, Julian date and quadratic effect of Julian date as independent variables.

	Estimate	Std. error	z value	2.5% CI	97.5% CI	*p* value
Intercept	4.821	0.085	56.690	4.654	4.987	<2e-16
Marine resource type	0.200	0.121	1.660	−0.037	0.437	0.097
Julian date*	−0.110	0.062	−1.760	−0.231	0.012	0.078
Julian date^2*	−0.133	0.054	−2.470	−0.238	−0.027	**0.013**

*The model was fitted with negative binomial error distribution and a log link. *z transformed variables. Bold text reflects statistically significant results.*

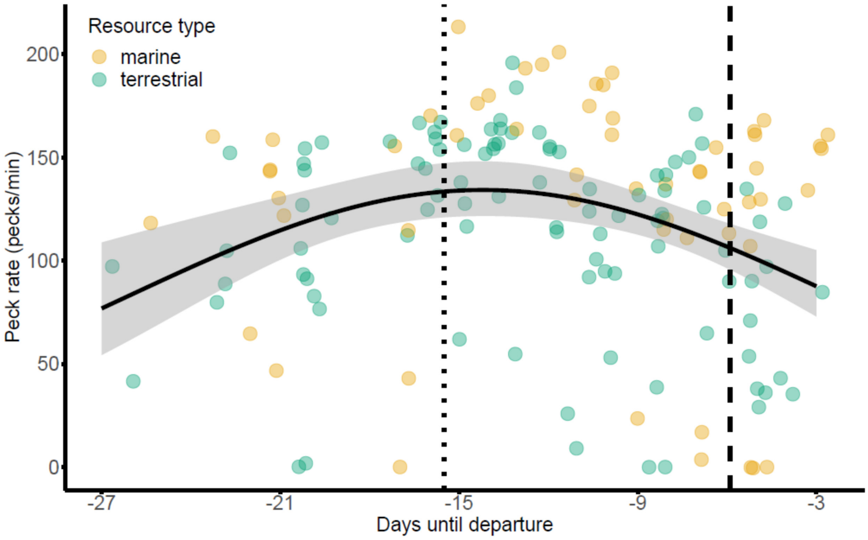

FIGURE 2 | Relationship between peck rates and days until mass departure of light-bellied brent geese from their spring staging site in Álftanes, Iceland. The resource type being fed on during focal observations is coloured as either yellow for marine (saltmarsh) or green for terrestrial (grassland) resources. The black line depicts the quadratic effect of date on peck rates and grey shading represents the standard error. The dotted line is the point of inflection, when the rate of weight gain begins to slow (x = 14–15/05/17). The dashed line represents the trough in the second derivative of the sigmoidal function, when the rate of weight gain begins to attenuate (x = 24/05/17).

to the previous three weeks (week 1 vs. week 4: $p < 0.001$; week 2 vs. week 4: $p = 0.044$; week 3 vs. week 4: p = 0.004).

Stable Isotopes

The best performing MAM for $\delta^{13}C$ included habitat type as response variable whereas the best performing MAM for $\delta^{15}N$ included habitat type as well as individual API. For C:N the best MAM included API and habitat type as well as their interaction as response variables. All three stable isotope measures showed a significant difference between samples collected on terrestrial or marine habitats, specifically $\delta^{13}C$ and $\delta^{15}N$ were both higher on marine sites (n = 130 observations, 59 individuals, $\delta^{13}C$: $r^2 = 0.35$; est. = −1.42, SE = 0.17, $p < 0.001$; $\delta^{15}N$: $r^2 = 0.29$; est. = −1.05, SE = 0.36, $p = 0.004$). We found $\delta^{15}N$ was statistically significantly higher in birds with higher API (n = 130 observations, 59 individuals, $\delta^{15}N$: $r^2 = 0.29$; est. = 0.33, SE = 0.11, $p = 0.004$, **Figure 3C**) and lower C: N ratios were found in faecal samples of individuals with a higher API (n = 130 observations, 59 individuals, $r^2 = 0.28$, est. = −1.72, SE = 0.76, $p = 0.02$, **Figure 3A**). However, the results show no significant relationship between an individual's API and habitat type they are feeding on (n = 130 observations, 59 = individuals; $r^2 = 0.83$, est. = 0.24, SE = 0.14, $p = 0.08$). Using a Tukey *post hoc* test we also found that individuals with higher API than the population average had significantly different $\delta^{15}N$ ratios in their faeces compared to those with lower than average API ($p = 0.03$, **Figure 4C**). Both individuals with above and below average API were feeding on similar resources with no significant difference in the $\delta^{13}C$ values ($p = 0.99$, **Figure 4B**), there was also no difference in the C: N ratio in faeces ($p = 0.16$, **Figure 4A**).

Wind Conditions

Geese experienced an average wind support of +1.23 m/s between 15 May and 5 June, indicating a tail wind (**Figure 5A**) and a crosswind of 5.21 m/s (**Figure 5B**). On the evening before departure the geese experienced a strong head wind (−6.78 m/s) but this dropped at midnight to −1.11 m/s and became a light tail wind (0.17 m/s) at 06:00 30/05/21. There was an above-average crosswind (6.89–7.51 m/s) present between midnight and 11:00 on the day of departure. Favourable wind support (i.e., tail wind) and crosswind conditions suitable for migratory departure were frequently present between 24 May when API attenuates and 30 May when the geese depart *en masse* and in the days following (**Figure 5**).

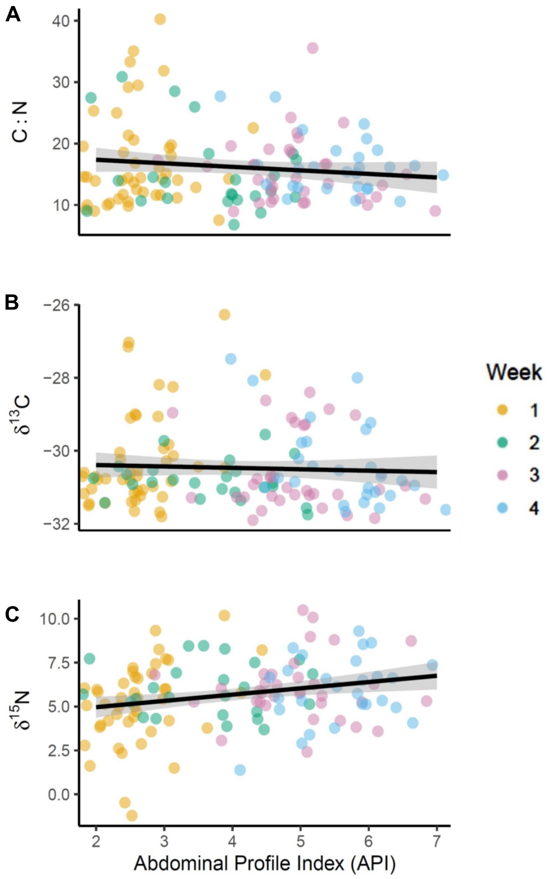

FIGURE 3 | Variation in stable isotope measures **(A)** C:N ratio, **(B)** δ^{13}C, and **(C)** δ^{15}N associated with weight gain by brent geese during spring staging in Álftanes, Iceland (03/05/2017–27/05/2017). Weight gain measured according to abdominal profile index (API). Data displayed by the week of spring staging when the faecal sample was collected, orange (week 1), green (week 2), purple (week 3), and blue (week 4). Linear regression with standard error (grey shading). An increase in API had a significantly negative effect on C:N ratio ($\chi^2{}_1 = 0.85$, $p = 0.039$, $r^2 = 0.28$) and no significant effect on δ^{13}C ($p = 0.36$, $r^2 = 0.37$). The δ^{15}N values were significantly influenced by an interaction between staging week and API ($\chi^2 1 = 8.10$, $p = 0.044$, $r^2 = 0.26$).

DISCUSSION

Light-bellied brent geese demonstrate behavioural and physiological flexibility during their one-month spring staging period in southwest Iceland. The results show that weight gain in brent geese begins attenuating approximately seven days prior to departure from Iceland, with females being on average fatter than their male partners (**Figure 1**). Despite early arrival at breeding grounds being a key driver of hatching success, individuals chose not to capitalise on favourable wind conditions occurring during the last week of staging (**Figure 5**). This suggests that environmental cues are not the only factor driving migratory departure. The observed behavioural changes (**Figure 2**) and stable isotope results across the month of staging (**Figures 3**, **4**) support the hypotheses that brent geese exhibit a period of hyperphagia followed by reduced foraging in response to migratory weight gain requirements. There is also evidence of protein reorganisation occurring prior to departure with a decrease in the C: N ratio (higher proportion of N in the faeces) and higher δ^{15}N (indicating protein catabolism) toward the end of the staging period. This supports the prediction that physiological adjustments are occurring in preparation for the upcoming flight and capital breeding life history strategy. Of course, there could be other explanations for such a pattern, for example, if resources were abundant and departure date was hardwired due to constraints on the breeding grounds. However, 2017 was a typical year in terms of arrival dates, feeding rates and habitat choice. Moreover, fluctuating conditions on route and at arrival on the breeding grounds would tend to suggest that there should be some ability to optimise departure decisions.

Behaviour

Throughout the month of spring staging in Iceland, light-bellied brent geese significantly changed foraging rates and locomotion behaviour in relation to the time of staging. Initially geese arrived with low API, however despite this, we observed low foraging rates. This is often explained by the "gut limitation hypothesis," whereby an individual experiences slow regeneration of digestive efficiency after a period of fasting (McWilliams and Karasov, 2005). The approximately 1,500 km non-stop migratory flight from Northern Ireland induces a period of fasting likely to cause atrophy of disused organs such as the digestive system. Regeneration of organs requires time and energy, hence an initial slow foraging period upon arrival in Iceland (McWilliams and Karasov, 2005). This has been observed in lesser snow geese, *Chen caerulescens caerulesces* where lower foraging rates were associated with individuals carrying atrophied digestive organs (Ankney and MacInnes, 1978). Furthermore, this hypothesis was also supported in passerine experiments, showing low food intake rates after a period of fasting even when food was offered *ad libitum* (Klaassen and Biebach, 1994; Hume and Biebach, 1996; Klaassen et al., 1997; Karasov and Pinshow, 2000; Karasov and McWilliams, 2005).

We found the time from arrival was the strongest predictor of variation in foraging rates during spring staging. After the initial slow start geese entered a state of hyperphagia, excessively eating in an effort to store enough energy to fuel the continuation of migration and initiation of breeding upon arrival in the High Arctic. As abdominal fat deposits increased so did the foraging rate but both foraging rates and fat gain decreased in the last period of staging, likely due to individuals approaching the target mass required to fuel migration and breeding. Additionally, it becomes more energetically advantageous to maintain a threshold weight as opposed to continue increasing bodyweight (Lindström, 2003), so in this last period before departure fatter individuals were observed sitting more. On average males had a lower threshold weight than females, potentially the result of mate guarding behaviour and a difference in energetic demand experienced by the sexes during long-distance migration and a capital breeding strategy. The reproductive success of female brent geese can change from 8 to 65% with an increase in their body mass at the breeding grounds (Inger et al., 2008). Light-bellied brent geese

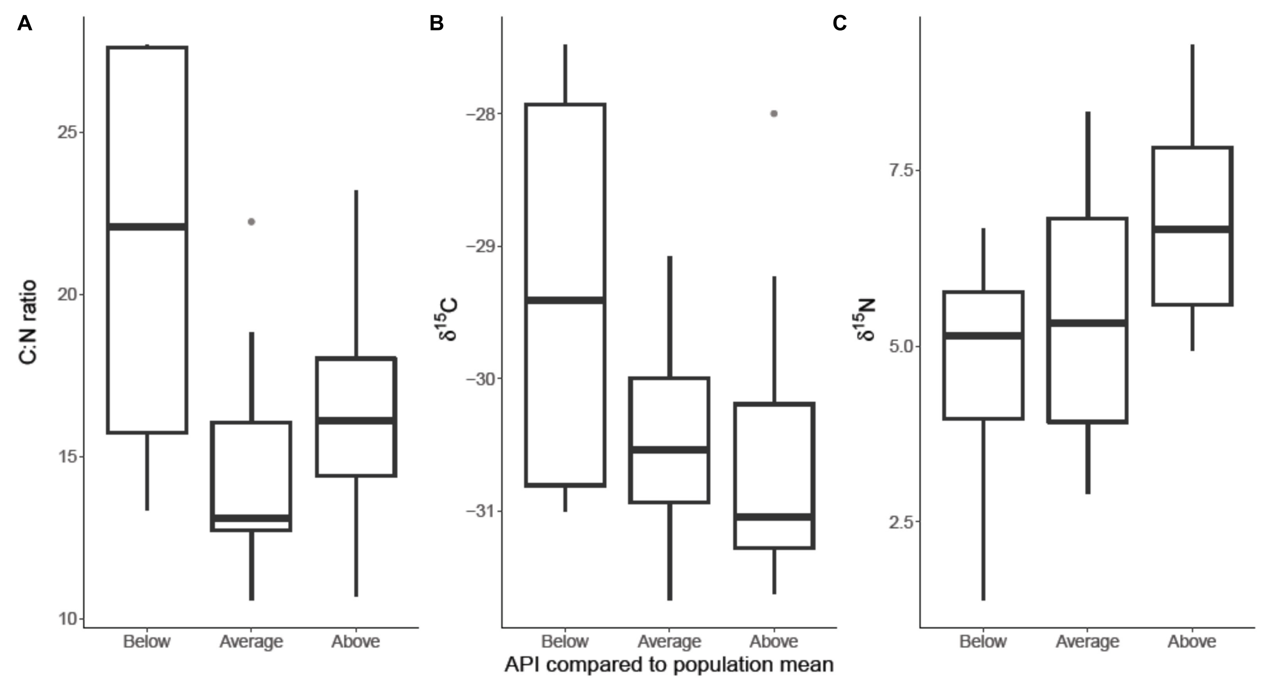

FIGURE 4 | Variation in stable isotope measures **(A)** C:N ratio, **(B)** δ^{13}C, and **(C)** δ^{15}N associated with body condition of brent geese during the final week of spring staging in Álftanes, Iceland (20/05/2017–27/05/2017). Body condition measured as above, below or at population average for abdominal profile index (API). In week 4 individuals with an above-average API excreted significantly higher δ^{15}N values than those with a below-average API (*Tukey post hoc*, $p = 0.025$).

from the adjacent Svalbard/Greenland population are known to lay eggs within a week of arriving (Clausen et al., 2003), highlighting the importance of accumulating large fat deposits prior to departing the spring staging site.

The delay in mass departure despite attenuation of weight gain by both sexes suggests that there are other physiological limitations prolonging the staging period in Iceland. In response to fasting and in-flight starvation waterfowl and wader migrants have been shown to experience protein turnover within their organs (Bauchinger and McWilliams, 2010). Lesser snow geese, a similar-sized waterfowl were found to atrophy organs during a 5–6 day period of decreased foraging rates (Ankney and MacInnes, 1978). This is also commonly seen in migratory wader species such as red knots, *Calidris canutus* found to have a pre-departure turnover of protein, with the digestive organs shrinking and flight muscles (i.e., pectoral) increasing in size (Piersma et al., 1999). This phenotypic flexibility is a potential explanation for the behavioural changes observed in the brent geese during their pre-departure week of spring staging.

Physiology

The stable isotope component of this study in conjunction with the behavioural observations provides further evidence of phenotypic flexibility occurring in the light-bellied brent geese during spring staging in Iceland. We found significant changes in the C:N ratio and δ^{15}N in the faeces of brent geese, in response to reaching peak abdominal fat. Both are indicators of a higher rate of protein turnover that would be expected in animals undergoing fasting and tissue-specific reorganisation, in this instance in preparation for the non-stop migratory flight to their breeding grounds in the Canadian High Arctic.

In comparison to other capital breeding migrants brent geese are physiologically constrained by a large energy requirement to body size ratio (Buchsbaum et al., 1986; Battley and Piersma, 2005). Their solely herbivorous diet has low nutrients and is high in structural components, with cellulose in plant cell walls making it hard to breakdown and digest (Buchsbaum et al., 1986). Therefore, they require a large gizzard and large small intestine to efficiently acquire nutrients and accumulate crucial energy deposits, constituting ∼95% lipids and ∼5% proteins, needed to fuel migration (Sedinger et al., 1989; Jenni and Jenni-Eiermann, 1998; Klasing, 1998; Battley and Piersma, 2005; Rozenfeld and Sheremetyev, 2016). Female geese in particular have a high energetic demand requiring significant fuel accumulation during the month of spring staging to rapidly initiate breeding on arrival and successfully breed. However, a large digestive system takes up crucial space within the abdomen and is metabolically costly during flight and capital breeding. Digestive organs constitute approximately 10% of a bird's lean mass making it a significant burden on wing load (Pierce and McWilliams, 2004). The measured decrease in C:N ratio in brent goose faeces associated with heavier individuals as the staging month progressed is a likely result of a physiological trade-off occurring. As adipose fat is accumulated in the abdomen we can infer that the digestive organs are compromised to maximise available space (Battley and Piersma, 2005). Waterfowl are known to compensate for the low nutrient concentrations in their herbivorous diet by having a long small intestine improving nutrient absorption and

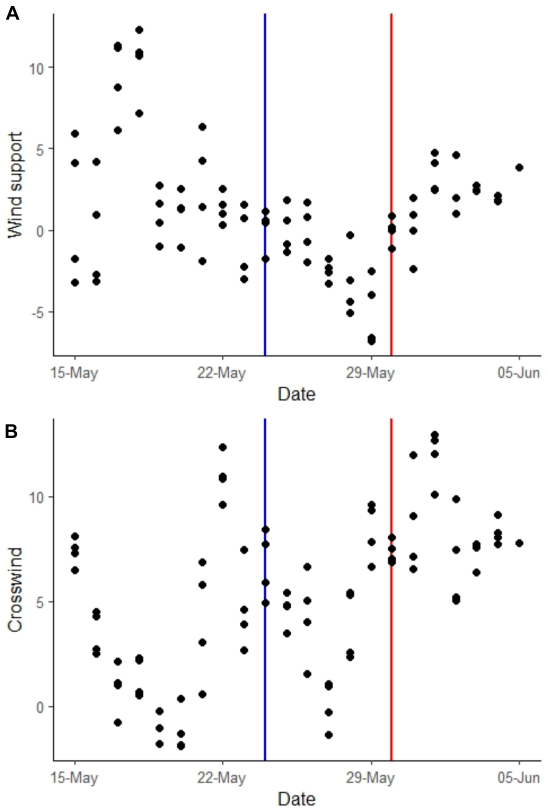

FIGURE 5 | Wind conditions experienced by light-bellied brent geese (LBBG) staging on the Álftanes peninsula between 15/05/17 and 05/06/17. The blue line is the date when LBBG weight gain attenuates (24/05/17) and the red line is the date of their mass departure (30/05/17). Wind conditions were calculated as either **(A)** wind support, with positive values indicating a tailwind and negative values a head wind and **(B)** crosswind was taken as an absolute value irrespective of direction. Calculated with a reference heading direction on the southeast coast of Greenland (65° 42′N, 37° 42′W).

also recycle excretory and endogenous nitrogen in the caecum, improving overall nitrogen balance (Sedinger, 1997; Barboza et al., 2008, p. 156). Given this, a compromised digestive system and resulting reduction in organ size will likely cause a reduction in assimilation efficiency causing the excretion of dietary nitrogen (Barton and Houston, 1993; Sedinger, 1997).

The results also show a significant increase in δ^{15}N of faecal samples as the month progresses and individuals accumulate abdominal fat stores. A higher δ^{15}N is usually indicative of an animal feeding at a higher trophic level (Bearhop et al., 2000; Inger and Bearhop, 2008). However, brent geese are strictly herbivorous and we did not observe a change in their resource use. A study by Fuller et al. (2005) confirmed that δ^{15}N values were not only influenced by dietary intake but also fluctuations in the body's nitrogen homeostasis, suggesting that the increase in δ^{15}N in the goose faeces might have an internal physiological explanation. Migratory birds are known to build, dispense and restore components of their body throughout their annual life history stages, strategically enhancing fuel storage and reducing flight costs (Fox and Kahlert, 2005). Empirical evidence from terminal studies on long-distance migratory water birds demonstrates pre-departure atrophy with up to 50% reduction in digestive tissues occurring at the staging site (Piersma et al., 1993; Jehl, 1997; Piersma and Lindström, 1997; Piersma and Gill, 1998).

The reorganisation of internal organs prior to migratory departure enables a bird to reallocate proteins away from the expensive disused digestive system into the synthesis of flight muscles (McLandress and Raveling, 1981; Jehl et al., 2015). When an animal's body is in a stable feeding state, assimilation of dietary protein tends to result in light ^{14}N being preferentially excreted, resulting in an increase in body tissue δ^{15}N, relative to the diet (Bearhop et al., 2000; Inger and Bearhop, 2008; Krausman and Cain, 2013). However, the enrichment of ^{15}N seen in the faeces of heavier brent geese is commonly found during periods of nutritional stress when higher rates of protein catabolism can often occur (Hobson et al., 1993). In this case, we have inferred that the increase in δ^{15}N represents a controlled reallocation of proteins in preparation for migratory departure.

An alternative explanation for the increase in δ^{15}N in the faeces is that the geese are entering a state of starvation in response to the low food intake, initiating the catabolism of proteins as a source of energy. However, this is unlikely as birds and mammals are known to prioritise lipid utilisation until fat stores drop below a critical limit (Jenni et al., 2000). For migratory bird species, this was shown to be as low as 5–10% of fat remaining and only then do they shift to catabolising protein to meet energy requirements (Cherel et al., 1988; Schwilch et al., 2002). Given that abdominal fat stores remain constant once a threshold weight is reached, it is unlikely that the protein catabolism measured in this study using stable isotope techniques is the result of foraging rates decreasing (i.e., starvation), rather shows phenotypic flexibility in the migratory light-bellied brent geese.

Despite female brent geese carrying a higher energetic burden upon reaching the breeding grounds, the sexes showed no difference between the δ^{15}N values and C:N ratio in their faeces. This highlights the significant cost of carrying potentially redundant organs and the importance of pre-departure protein catabolism and synthesis in an effort to reduce wing load and improve flight efficiency.

CONCLUSION

In this study, we used a non-invasive sequential sampling method to track behavioural and physiological changes in light-bellied brent geese across the month of spring staging. Our results show phenotypic flexibility of this Arctic breeder, in response to the high energetic demands of long-distance migration and a capital breeding life history strategy. A decrease in foraging and locomotion rate in the last week of staging coincided with the attenuation of weight gain. During this last week, we also found fatter individuals had a lower C:N ratio and higher δ^{15}N values in their excretion. All these factors support the prediction that it is beneficial for brent geese to undergo a reorganisation of internal protein, changing from a body prioritising resource acquisition for fat deposition, to one promoting efficient flight. It should be noted that this study was only based on data collected in one spring staging season meaning that it is impossible to make assumptions on the repeatability of the occurrence of the behavioural and stable isotope patterns observed in this study. However, we have no reason to suspect that it was an atypical season. Future directions to improve our understanding of phenotypic flexibility during avian migration should include the non-invasive measurement of gut size throughout the staging period (i.e., using ultrasonography techniques (Vézina et al., 2012). By combining such measurements with behavioural studies and stable isotope data a more complete picture of the phenotypic flexibility during migratory staging could be gained.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the CLES Penryn Ethics Committee.

AUTHOR CONTRIBUTIONS

SB, TH, JS, and XH conceived the project. TH, JS, and SL carried out the fieldwork. TH, JS, and XH analysed the data. TH and JS lead the writing of the manuscript, with contributions from all authors. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.749534/full#supplementary-material

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