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RESEARCH ARTICLE

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Agricultural pastures challenge the attractiveness of natural saltmarsh for a migratory goose

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Abstract

1. Broad-scale land conversions and fertilizer use have dramatically altered the available staging area for herbivorous long-distance migrants. Instead of natural land, these birds rely increasingly on pastures for migratory fuelling and stopover, often conflicting with farming practices. To predict and manage birds' future habitat use, the relative advantages and disadvantages of natural (e.g. saltmarsh, intertidal) versus anthropogenic staging sites for foraging need to be understood.

2. We compared the migratory staging of brent geese on saltmarsh and pasture sites in spring. Food quality (nitrogen and fibre content), antagonistic behaviour, and body weight were quantified at nearby sites in simultaneous seasons. Individuals were tracked with high-resolution GPS and accelerometers to compare timing of migration and time budgets during fuelling.

3. On pastures, birds rested more and experienced higher ingestion rates, similar or superior food quality and reduced antagonistic interactions than on saltmarsh.

4. Brent geese using fertilized grasslands advanced their fuelling and migration schedules compared to those using saltmarsh. Pasture birds reached heavy weights earlier, departed sooner, and arrived in the Arctic earlier.

5. Intertidal mudflats were frequently visited by saltmarsh birds during the day, and available food there (algae, some seagrass) was of higher quality than terrestrial resources. Availability of intertidal resources was an important factor balancing the otherwise more favourable conditions on pastures relative to saltmarsh.

6. *Synthesis and applications*. Disadvantages of longer foraging effort, more antagonistic interactions and delayed fuelling schedules on traditional saltmarshes may cause geese to exchange this traditional niche in favour of pastures, especially in a warming climate that requires advancement of migratory schedules. However, due to its high quality, intertidal forage can complement terrestrial foraging, potentially removing the incentive for habitat switches to pastures. The relatively high quality of green algae and seagrass, and birds' remarkable preference for these resources when available, provides a key for managers to create landscapes that can sustain this specialist's intertidal lifestyle. To keep natural habitats attractive to staging geese with the

purpose of preventing conflicts with farming practices, management actions should focus on conservation and restoration of saltmarsh and especially intertidal habitat.

KEYWORDS

accelerometer, brent geese, GPS tracking, habitat switching, human–goose conflict, migration, pastures, saltmarsh

1 | INTRODUCTION

Human activity is altering our planet's surface in rapid and pervasive ways. Over 80% of the earth's land mass is now under direct human influence (Sanderson et al., 2002), with croplands and pastures occupying over 40% of the total area (Asner, Elmore, Olander, Martin, & Harris, 2004; Foley, 2005). Migratory birds need to navigate these human-altered landscapes during their seasonal migration and depend on them as alternatives to lost natural habitat. Especially, agricultural land plays an important role in supporting migratory bird communities year-round: pastures provide wintering and breeding grounds to meadow passerines, waterfowl and waders (Knopf, 1994); rice fields (Elphick, 2015; Lourenço, Mandema, Hooijmeijer, Granadeiro, & Piersma, 2010) and salt pans (Masero, Pérez-Hurtado, Castro, & Arroyo, 2000) act as important alternative stopover for shorebirds, and crane and goose populations make extensive use of waste crop in winter (Ma, Cai, Li, & Chen, 2010; Stafford, Kaminski, Reinecke, & Manley, 2006; Tourenq et al., 2001).

While agricultural intensification has led to precipitous declines of several farmland birds (Chamberlain, Fuller, Bunce, Duckworth, & Shrubb, 2000; Donald, Green, & Heath, 2001), geese are one of the few species groups that are successful in exploiting agricultural monocultures. By feeding on specially bred high-energy cereal, root and grass crops, in combination with instated hunting bans and improved protection of crucial stopover and wintering sites, populations of most goose species have recovered over the last 50 years (Abraham, Jefferies, & Alisauskas, 2005; Fox & Abraham, 2017; Fox et al., 2005). Their reliance on human landscapes is more apparent than ever, and conflicts between goose foraging and human farming practices continue to increase (Fox & Madsen, 2017). In addition to the effect of population growth *per se*, migratory geese cause increasing crop damage because fertilizer application combined with warming springs has advanced crop phenology towards the migratory staging periods. As a result, Arctic migrants are nowadays still present when the first spring cutting or harvest is due at temperate latitudes (Fox, Elmberg, Tombre, & Hessel, 2016).

Besides agricultural sources, natural areas remain important for geese, especially for species with a traditional coastal niche, like brent geese *Branta bernicla*. Brent geese breed on wet Arctic tundra, but forage on seagrass *Zostera* spp. and macroalgae *Ulva* spp. beds during the autumn migration and winter. Along the East-Pacific flyway, where these resources are most abundant, brent geese rely on seagrass and algae also during spring fuelling. Along the Atlantic flyways (both West and East), where seagrass abundance has seriously declined (Folmer et al., 2016), populations also make use of alternative terrestrial resources during the course of winter and spring, such as saltmarsh, pastures and winter wheat (Inger et al., 2006; McKay, Langton, Milsom, & Feare, 1996; Summers, 1990; Tubbs & Tubbs, 1982; Vickery, Sutherland, Watkinson, Lane, & Rowcliffe, 1995; Ward et al., 2005).

In this study, we focus on the population along the East-Atlantic flyway, the dark-bellied brent goose *Branta b. bernicla*. Previous studies showed that dark-bellied brent geese (brent geese, hereafter), switched to feeding on saltmarsh in May, after feeding on pasture in March and April. Plant growth started later on the saltmarsh, and as a result, plant quality became as high (Eichhorn, Meijer, Oosterbeek, & Klaassen, 2012; Prins & Ydenberg, 1985) or, according to some, even higher on the saltmarsh in May (Boudewijn, 1984). Preference for the saltmarsh later in spring was further explained by the lack of disturbance, increasing foraging time and reducing energy expenditure on the saltmarsh (Prins & Ydenberg, 1985; Riddington, Hassall, Lane, Turner, & Walters, 1996). Disturbance in the pasture habitat likely had an indirect effect as well: it prevented brent geese from concentrating on specific pasture parts, where they otherwise could keep the grass short and thereby maintain a high food quality (Bos, van de Koppel, & Weissing, 2004; Spaans & Postma, 2001).

From 2000 onwards, a new policy was implemented in the Netherlands that stopped deliberate scaring of brent geese in the majority of pasture habitat frequented by brent geese in early spring. This immediately led to more and extended visits of brent geese to the pasture habitat, while other individuals still fuelled on the saltmarsh (Bos & Stahl, 2003). In this study, we aim to uncover which aspects of natural stopover sites, specifically natural saltmarsh, sustain the use of this habitat by migratory geese. We did this by comparing fuelling of brent geese on nearby saltmarsh and pasture staging sites. We simultaneously quantified, for both habitats, individual grazing time budgets, defecation rate and dropping weight (as proxies for ingestion rate, the rate at which biomass is grazed and swallowed), food quality, antagonistic behaviour, and their combined effect on body condition and timing of migration of brent geese. Based on the comparison, we identify management actions for keeping natural habitats attractive to brent geese.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study sites were located on two barrier islands of the Dutch Wadden Sea, the agricultural pastures of island Terschelling (53.38N, 5.29E) and the early successional saltmarsh of Schiermonnikoog

(53.49N, 6.30E). Plant sampling and behavioural observation programs were run in parallel at both sites from March 26 to June 7 2013. The pasture site consists of 14 km^2 contiguous agricultural grasslands stretched over a distance of 10 km. Fields are used mainly for dairy farming and livestock grazing but are managed as a goose and meadow bird refuge in spring. It is actively fertilized but free from scaring, disturbances or hunting, and mowing is postponed until early June. The back-barrier marsh of Schiermonnikoog extends over a distance of 6 km. It is managed as a nature reserve and is closed to the public in spring. Along the south-eastern 2–3 km, new marsh continues to form. The pristine young successional stages are intensively grazed by brent geese (Kuijper & Bakker, 2005), making it an important natural staging site for this species. No livestock grazing occurs on the young stages of the marsh.

2.2 | Individual GPS tracking: Behavioural classification and time budget analysis

In spring 2012, brent geese were captured using canon netting both at the pasture site (53.37270N, 5.26922E) and at the saltmarsh site (53.4955N, 6.29229E). Individuals were colour-ringed with unique codes, weighed within a few hours after capture, and sexed by cloacal examination. In total, 30 adult male brent geese were tagged with UvA-BiTS GPS trackers (Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013), which were attached as a backpack using nylon strings inserted in 4-mm wide silicon tubing (Lameris et al., 2018). Twenty-one individuals were tagged at the pasture site and nine at the saltmarsh site. Trackers were set to collect GPS fixes every hour down to every 5 min depending on available solar power. Following each GPS fix, we collected triaxial accelerometer data to quantify the birds' foraging activity. In next spring (2013), six and four birds returned with working tags to fuel at the pasture and saltmarsh site, respectively, and no switches between the two habitat types were observed between years, nor within seasons (Fokkema et al., 2017). Because it may take some weeks for waterfowl to get accustomed to a tag (Kölzsch et al., 2016; Nuijten et al., 2014), we used this following spring for quantifying time budgets. Our birds frequently preened in the days after capture, but such behaviour was no longer observed next year.

As a measure of activity, we used the accelerometer's vectorial sum of dynamic body acceleration α (Qasem et al., 2012), defined as the root of the sum of the three acceleration variances for each axis: $\alpha = \sqrt{(\sigma^2_x + \sigma^2_y + \sigma^2_z)}$, where σ_x, σ_y, and σ_z are the SD of acceleration in the surge, sway and heave directions in units of g_0, the earth's standard gravity, and using a 20-Hz signal over 7/20 s. The probability density histogram for α for birds located on the grasslands is shown in Figure S1. The peak at $\alpha = 0.015\ g_0$ corresponds to cases where the bird is standing still, whereas the peak at $\alpha = 0.15\ g_0$ corresponds to cases where the bird is actively foraging. We categorise a bird as inactive when $\alpha < 0.04\ g_0$ or active when $\alpha > 0.04\ g_0$. The threshold was found by decomposing the distribution into two gamma distribution components, equalling the point where these two components intersect at the same probability. Flying was detected using a

threshold of $\alpha > 0.6\ g_0$. Using 1 hr of video data on four black brent geese (Branta b. nigricans) GPS-tagged in captivity, we verified that the threshold in α and sampling duration accurately distinguished inactivity from active behaviour (visually confirmed inactive resting $\alpha = 0.015 \pm 0.01$).

To determine whether birds were roosting on water, we used a bathymetric map of the Dutch Wadden Sea (cycle 5 map at 20 m resolution) and tidal water heights (every 10 min) provided by Rijkswaterstaat, Ministry of Infrastructure and Water Management, the Netherlands. Mudflats were assumed to be flooded when the bathymetric height at the bird's position was below the water height measured by the nearest tidal station (pasture, west-Terschelling 53.36305N 5.22003E; saltmarsh, Schiermonnikoog, 53.46894N 6.20291E).

Combining accelerometer activity and location, we classified GPS fixes into 12 categories: fly, land active, mudflat active, on water, land rest, mudflat rest, each split out by day and night. For each individual, daily time budgets were calculated as the time spent in each category.

2.3 | Field observations: Faecal excretion and conspecific interaction rate

Antagonistic behaviour was quantified by scoring interactions between randomly picked focal individuals and other brent geese. Other goose species were uncommon at our study sites, and only intraspecific interactions were observed. We defined an interaction as a direct confrontation between two birds, ranging from threats with lowered head and neck to active chases with flapping wings (cf. Stahl, Tolsma, Loonen, & Drent, 2001). Interactions were classified as wins, losses or draws (if no dominant bird in the interaction could be identified). For continuous observation bouts on individuals of at least 5 min (median 13 min), we calculated the interaction rate as the numbers of combined wins, losses and draws divided by the bout length (Figure 2 bottom). We recorded 1,415 interactions during 360 observation bouts of in total 121 hr on pastures, and 441 interactions during 102 bouts of in total 30 hr on saltmarsh.

To determine the seasonal trend in dropping rate (Figure 2), we timed 568 (pasture) versus 133 (saltmarsh) intervals between defecation events of the same focal birds during interaction observations. Interval data were fitted to a probability density function that accounted for the nonzero chance that an observer failed to see a dropping be excreted (Dokter et al., 2017). Dropping and interaction observations were grouped into 2-week periods according to the mid-points between the dates of vegetation sampling (see below).

2.4 | Vegetation sampling and analysis

Grass and excreta were sampled in multiple transects (4 on saltmarsh, 6 on pasture, 4–5 stations each) of increasing distance to the intertidal, such that fields exposed to different grazing intensities

and elevational gradients were included in the programme (see Fokkema et al., 2015) and (Dokter, Fokkema, Bekker, et al., 2018) for details on the sampling scheme). At each station, a 1-m^2 exclosure was put in place on March 13 2013, which was moved by several metres into a new position during visits every 2 weeks. Plant material was collected from inside the exclosure on March 26 (pasture site only, as saltmarsh was still bare), April 10, April 21, May 8, and May 21. The pastures consisted of monocultures of *Lolium*, and only this single species was collected per station. On saltmarsh brent diet is more diverse, as has been well established in earlier studies at this site. On Schiermonnikoog brent geese forage mostly on *Plantago maritima*, *Triglochin maritima*, *Puccinellia maritima*, and *Festuca rubra* (Fokkema et al., 2015; Prop & Deerenberg, 1991), which was the potential saltmarsh diet considered for this study. During each field visit, we quantified grazing pressure per field (in droppings per m^2) by counting droppings in five circles of 4 m^2, which were cleared each visit and of which the centres were marked by inconspicuous 5 cm protruding sticks. From each circle, two droppings were collected as fresh as possible. Intertidal forage was sampled on mudflats at Uithuizerwad (53.47N 6.75E) on June 18, one of the few areas in the Dutch Wadden Sea where seagrass *Zostera noltii* still occurs, and where brent geese frequently forage (van der Heide et al., 2012). Sea lettuce *Ulva lactuca* was also sampled here. Plant and dropping material was oven-dried at 60°C for 24 hr directly after collection, and ground through a 1 mm sieve, after weighing droppings individually.

A random selection stratified by period yielded 25 pasture and 60 saltmarsh samples which were chemically analysed for acid detergent fibre (ADF) (Van Soest, Robertson, & Lewis, 1991). The chemical ADF analyses were used as a calibration dataset for estimating ADF concentrations of the full dataset (135 plant samples pasture, 116 samples saltmarsh) by near-infrared reflectance spectroscopy on a Bruker MPA FT-NIR analyser using the OPUS 7.0 software package (Foley et al., 1998). All samples were analysed for total nitrogen using a Thermo Scientific FLASH 2000 elemental analyser. ADF and nitrogen content are expressed as mass percentages on ash-free dry mass basis. Period averages of these quantities were calculated as an average over stations weighted by the grazing pressure of each field in that period. This weighting guaranteed that ADF and nitrogen values represented the fields that were used for foraging by the geese, and not the unused fields.

2.5 | Statistics

Temporal trends and differences between sites in time budgets were analysed using a linear mixed model for each time budget category (Table 1), using the lme function of R-package nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2017). We considered date (unit: days since January 1 2013), site and their interaction as fixed effects, and individual as random effect (random date slope and intercept), as in activity ~ date + site + date:site + (date|ID). The most parsimonious model was selected using the Akaike information criterion for models fitted by log-likelihood maximization (ML). Site effects (terms site and date:site) were retained only if including these terms significantly

improved the model according to a likelihood ratio test against a null model without these terms. We applied a Bonferroni correction to these likelihood ratio tests to correct for multiple comparisons, by multiplying *p*-values by the number of categories considered (12). Parameter estimates were obtained from a fit by restricted likelihood maximization (REML).

Dropping weights, interaction rates, and plant quality measures were compared using Mann–Whitney *U* tests. Since plant quality was measured for different plant species, we adjusted *p*-values by a Bonferroni correction for multiple comparisons between species within each month. To test for body weight differences between sites, we first accounted for the 5–6 day difference in catching date, by applying a correction of +60 g to the saltmarsh bird weights, assuming a 10 g/day weight gain (Ebbinge & Spaans, 1995). Each sex was tested separately. We calculated the principal components of the structural size measurements wing length and head length against body weight. We then tested for a significant effect of site in a linear model for body weight, including the first principal component (PC1) as a predictor to correct for structural body size.

3 | RESULTS

Individual high-resolution time budgets show that brent geese staging on saltmarsh spent more time actively foraging than birds on pasture (Figure 1, green active, red idle), on average 2.3 and 1.7 hr more in April and May, respectively, cf. Table 1. This table shows mean time budgets for April and May averaged over individuals, and a temporal trend analysis (with trends differing between habitats indicated in bold). Pasture birds were frequently idle for short periods, indicating they were resting or taking digestion pauses; this idling increased over the season (Table 1). Interestingly, saltmarsh birds complemented foraging on land with additional daytime foraging trips to the intertidal during low tide (Figure 1) and spent overall more active time in the intertidal zone, especially during the day (Table 1). Such daytime intertidal foraging trips were not observed for pasture birds. Pasture birds spent more time flying than saltmarsh birds, but daily flight time decreased to below half an hour over the season in both habitats (Table 1).

Both the weight of individual faecal droppings, and the rate at which droppings were excreted, were lower on saltmarsh than on pasture (Figure 2 top). The rate of excretion of undigested plant material was therefore lower at the saltmarsh. Saltmarsh was also a more antagonistic environment than pasture, as shown by a higher frequency of aggressive interactions in April (Figure 2 bottom).

Food quality was assessed by the food's nitrogen content and ADF content (afdm basis), which are proxies for protein content and fibre content respectively. Food quality was assumed to increase with protein content and decrease with fibre content (Prop & Vulink, 1992). Food quality values are shown in Figure 3, with mean and *SD* values given in Table S1. The quality measures of pasture grass were compared in a pair-wise fashion to each of the available food resources sampled on the saltmarsh and intertidal (Figure 3, pairs significantly different

TABLE 1 Trend analysis of individual brent goose time budgets. Time budgets are given as mean (and SD) among individuals in hours per day. Activity categories with a significant site effect (variables Pasture and/or Date:Pasture) in a mixed model analysis are highlighted in bold (unit Date: days since 1 January 2013). Model analysis gives fixed effect estimates (and SE) by REML

Activity		Time budget April (hr/day)		Time budget May (hr/day)		Model analysis			
		Pasture	Marsh	Pasture	Marsh	Intercept	Pasture	Date	Date:Pasture
Day	**Fly**	0.5 (0.2)	0.3 (0.2)	0.37 (0.06)	0.26 (0.01)	0.95 (0.17)***	0.17 (0.04)**	−0.006 (0.001)***	
Day	Land active	7.3 (3.3)	9.7 (1.7)	10.1 (0.8)	11.2 (0.9)	3.1 (0.8)***		0.052 (0.006)***	
Day	**Mudf. active**	1.8 (0.6)	1.7 (1.5)	1.1 (0.2)	1.7 (1.0)	0.4 (1)	2.5 (1.2)	0.014 (0.008)	−0.026 (0.009)**
Day	**Active total**	9.1 (3)	11.4 (2)	11.2 (0.8)	12.9 (0.9)	3.9 (1.3)**	1.8 (1.4)	0.063 (0.009)***	−0.02 (0.01)*
Day	On water	1.2 (0.5)	0.4 (0.6)	0.56 (0.08)	0.5 (0.5)	−0.3 (0.8)	4.8 (0.9)	0.007 (0.006)***	−0.037 (0.007)***
Day	**Land rest**	1.0 (0.6)	1.6 (0.6)	2.8 (1.1)	1.5 (0.7)	2.6 (0.9)**	−9 (1)***	−0.008 (0.007)	0.079 (0.008)***
Day	Mudflat rest	1.1 (0.2)	0.9 (0.4)	0.8 (0.1)	0.5 (0.2)	2.3 (0.4)***		−0.011 (0.003)***	
Night	Fly	0.08 (0.06)	0.1 (0.1)	0.09 (0.04)	0.08 (0.03)	0.08 (0.07)		0.0000 (0.0006)	
Night	Land active	0.15 (0.08)	2.2 (0.6)	0.13 (0.06)	1.4 (0.5)	0.9 (0.4)*		−0.003 (0.002)	
Night	Mudf. active	2.4 (0.9)	1.3 (0.3)	1.9 (0.5)	1.5 (0.5)	3.5 (0.4)***		−0.015 (0.003)***	
Night	Active total	2.6 (0.9)	3.5 (0.6)	2.0 (0.5)	2.9 (0.5)	4.3 (0.5)***		−0.016 (0.004)***	
Night	**On water**	4.4 (0.6)	0.6 (0.7)	3.4 (0.5)	1.0 (0.5)	−3 (1)*	11 (2)***	0.04 (0.01)***	−0.07 (0.01)***
Night	Land rest	0.05 (0.04)	2.0 (0.7)	0.04 (0.03)	1.4 (1.0)	0.7 (0.4)		−0.002 (0.003)	
Night	**Mudflat rest**	4.2 (3.3)	3.2 (0.7)	2.8 (0.4)	3.2 (1.5)	11 (1)***	−7 (2)**	−0.07 (0.01)***	0.06 (0.01)***

Note. Significance of explanatory variables for the selected model are indicated by stars (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$ according to a *t*-test. Empty cells indicate including the term in the model was not supported by the data.
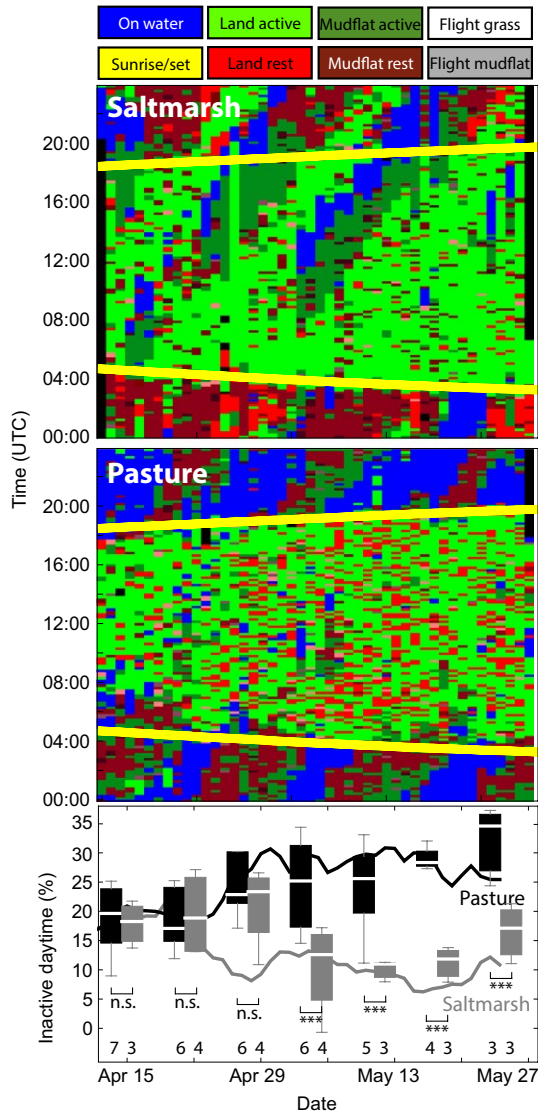
FIGURE 1 Example of the activity of brent geese for an individual on saltmarsh (top) and on pasture (middle). Yellow lines indicate sunrise and sunset. Daytime inactivity for these two individuals is given in the lower panel as solid lines (saltmarsh grey, pasture black). Daytime inactivity for all individuals is summarized as boxplots of individual 1-week-averaged daytime inactivity. Pairwise difference between habitats in these inactivity times were tested by a Mann–Whitney U test (n.s. not significant, ***p < 0.001)
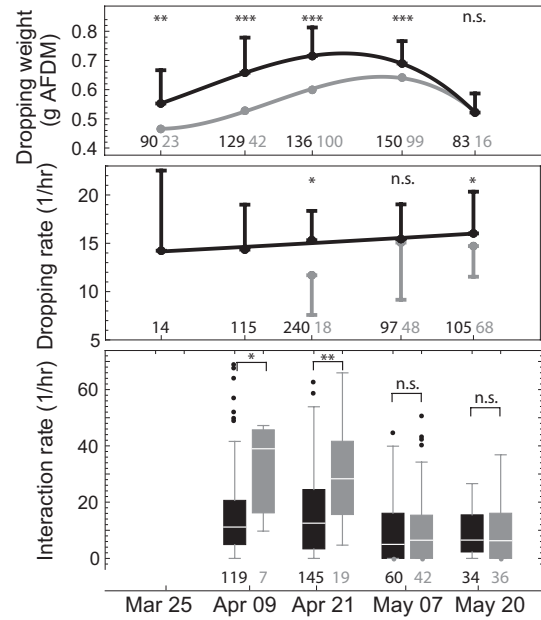

FIGURE 2 Grazing parameters and interactions compared between geese in saltmarsh (grey) and pasture (black) habitat. Top: seasonal trend in mean dropping mass. Middle: dropping rates estimated from dropping intervals recorded for individual geese. Bottom: number of antagonistic interactions per hour observed on focal geese during dropping rate observations. Significance of pairwise comparison between habitats for each period is indicated with stars (*p < 0.05, **p < 0.01, ***p < 0.001), using a Mann–Whitney U test for dropping weight and interaction rate, and a likelihood ratio test for dropping rate following (Dokter et al., 2017)

indicated by connecting brackets). The quality proxies for terrestrial plants in the diet of geese on saltmarsh never exceeded the values measured for fertilized grasses on pasture (Figure 3) in the 2 months considered (April and May). In later spring (May), only the rarer food items (*Plantago*, *Triglochin*) maintained comparable quality levels to pasture grasslands, while the more common food items (*Festuca*, *Puccinellia*) were of lower quality relative to fertilized grass (cf. Table S1. *Festuca*: N 0.7 ± 0.3% lower, ADF 4.2 ± 1.0% higher; *Puccinellia*: N 1.2 ± 0.2% lower, ADF 5.8 ± 1.4% higher). Interestingly, intertidal forage (*Zostera*, *Ulva*) were the only resources with a higher quality measures than terrestrial pasture grass (*Zostera*: ADF 7.1 ± 0.2% lower, N 0.1 ± 0.7% higher; *Ulva*: ADF 11 ± 1% lower). For *Ulva*, no N content

was determined in this study, but high protein content has been reported for *Ulva* in other studies (e.g. Ortiz et al., 2006).

Catches on saltmarsh and pasture showed that by mid-May pasture birds were in higher body condition than saltmarsh birds (Figure 4). This advanced fuelling schedule also translated in earlier departures from pastures than saltmarshes in both years that we tracked individuals (Figure 5). Pasture birds remained ahead of saltmarsh birds during migration up to 3,500 km from the spring staging sites.

4 | DISCUSSION

Nearly all foraging parameters in our comparative analysis pointed towards more favourable fuelling conditions on pastures than on saltmarsh. We found that birds foraging on saltmarsh spent a substantially longer active foraging time per day compared to birds foraging on pasture. A high food biomass availability, combined with a high quality, led to limited aggressive interactions on pastures, and these factors together likely translated into a superior ingestion rate. These ingestion rates were probably high enough for birds to approach their digestive bottleneck, explaining the frequent short resting periods most likely used for digestion. Such idling periods were much less common on saltmarsh, suggesting that saltmarsh birds were more ingestion-limited than digestion-limited. Birds
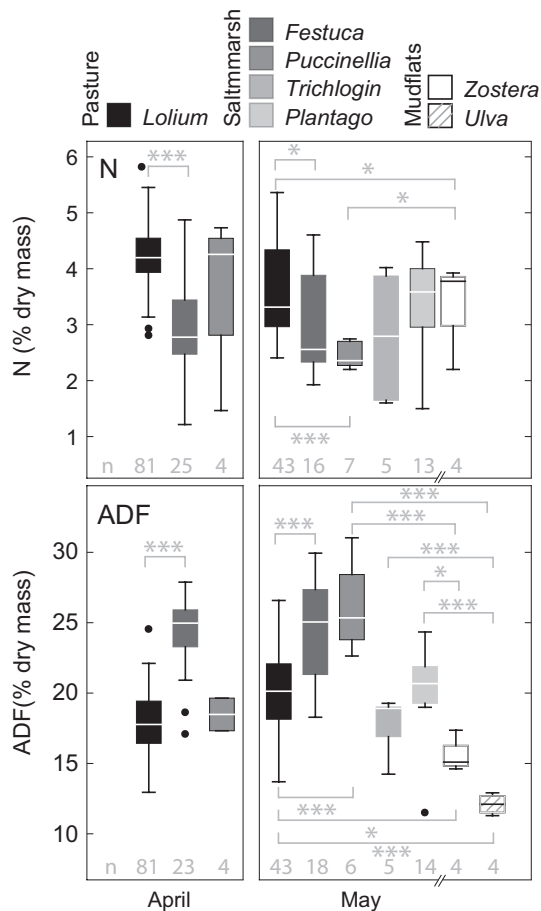
FIGURE 3 Nutritional quality measures (nitrogen content N in top panels, acid detergent fibre ADF in bottom panels) in April (left panels) and May (right panels) for food resources on pastures (black), saltmarshes (greyscales) and mudflats (white and white-shaded). High quality resources are assumed to have high N and low ADF. Significant pair-wise comparisons are indicated by brackets and associated significance level by stars according to a Mann–Whitney U test (*$p < 0.05$, ***$p < 0.001$, adjusted by a Bonferroni correction for multiple comparisons within each month). Nutritional quality of pasture resources (Lolium) was comparable or higher compared to saltmarsh resources both in April (Festuca N: $U_{81,25} = 1,693$ $p < 0.001$, Festuca ADF: $U_{81,23} = 104$, $p < 0.001$) and May (Festuca N: $U_{43,16} = 494$, $p = 0.01$, Festuca ADF: $U_{43,18} = 144$, $p < 0.001$, Puccinellia N: $U_{43,7} = 281$, $p < 0.001$, Puccinellia ADF: $U_{43,6} = 21$, $p < 0.001$). Intertidal resources (Zostera, Ulva) were of highest quality, with a higher nitrogen content and lower fibre content than pasture resources in May (Zostera N: $U_{43,4} = 277$, $p = 0.017$, Zostera ADF: $U_{43,4} = 273$, $p = 0.02$, Ulva ADF: $U_{43,4} = 324$, $p < 0.001$)

needed more time to collect their food, likely because high-quality resources are more patchily distributed on a saltmarsh. This time pressure also explains why they were more involved in antagonistic interactions than the geese foraging on pasture (Van Gils & Piersma, 2004). Saltmarsh vegetation is highly heterogeneous and brent geese can fight over patches rich in preferred plant species (Prop & Deerenberg, 1991), whereas pasture vegetation is very homogeneous. Easy access to high quality food on pastures likely allowed
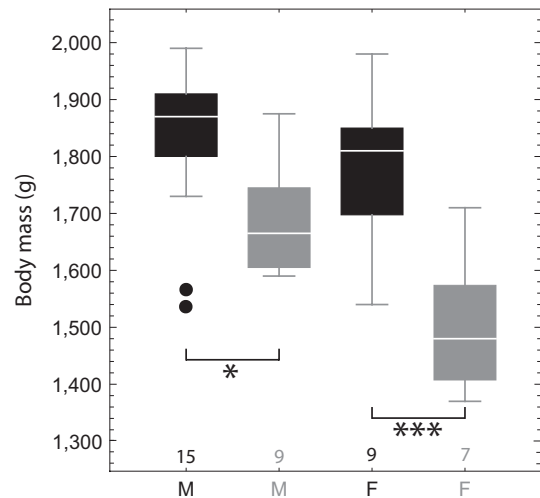

FIGURE 4 Body weight of adult male (M) and female (F) brent geese on pastures (black) and saltmarsh (grey) in mid-May. Catches dates (2012): pasture 15/16 May (n = 22), saltmarsh 10 May (n = 16). Stars indicate significant differences at 0.05 confidence level after correction for structural body size differences and the 5–6-day time difference between captures (see methods last paragraph). Males: $F_{1,21} = 7.8$, $p = 0.01$, Females: $F_{1,13} = 22.0$, $p < 0.001$

for earlier and faster fuelling rates, which explains the earlier weight gain and earlier migration of geese foraging on pastures.

Our results explain why nowadays many brent geese prepare for migration on pastures. While in the past frequent disturbance in pastures might have caused saltmarsh to be the preferred habitat (Prins & Ydenberg, 1985; Riddington et al., 1996), nowadays, with a lower disturbance regime in the pasture habitat and given our results, it may seem surprising that birds still return to saltmarsh. We cannot exclude the possibility that birds currently fuelling on saltmarsh mostly follow tradition, which is common for geese (Fox et al., 2005; Kanarek, Lamberson, & Black, 2008), and that birds return to the same historical stopover site even though conditions elsewhere may have become better. The alternative explanation that brent geese are pushed out of agricultural pastures to saltmarshes is considered unlikely, since pastures are abundantly available, such that density dependence is probably not playing a role in habitat choice (Fox et al., 2005). Also, no support was found for the hypothesis that saltmarsh vegetation provides nutrients or essential amino acids that cannot be obtained on pastureland (Eichhorn et al., 2012). Geese thus seem largely released from limitations by nutrients (Dokter, Fokkema, Bekker, et al., 2018; Fox & Abraham, 2017), at least in relatively mild temperate winter weather. An alternative reason that brent geese persist on saltmarsh may be that the pay-offs are eventually the same. Although we had indications of better fuelling conditions on pasture, a previous comparison of brent geese preparing for migration in pasture and saltmarsh habitat did not reveal any differences in reproductive success (Spaans & Postma, 2001). Such a difference might be expected since brent geese are capital breeders (Spaans't Hoff, van Veer, & Ebbinge, 2007), in which body
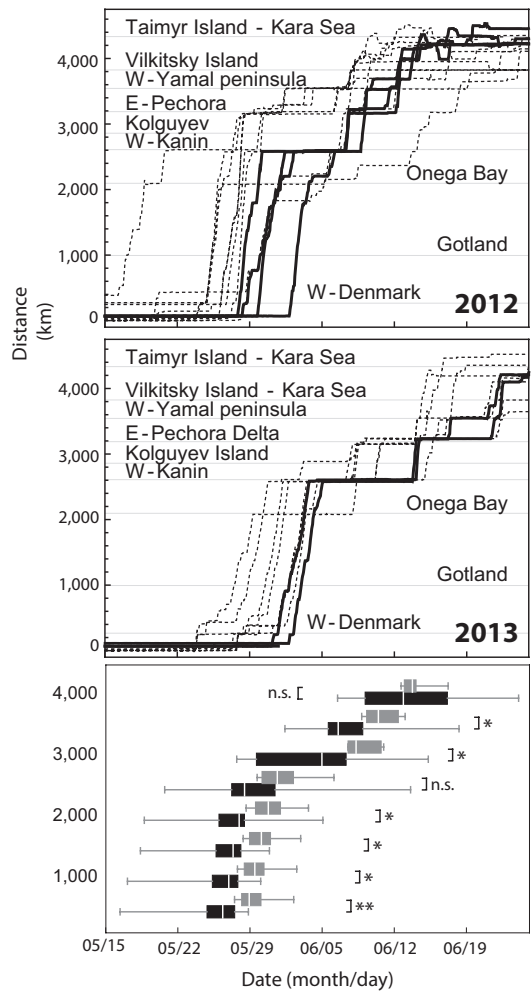
FIGURE 5 Timing of migration in 2012 (top) and 2013 (middle) for pasture birds (dotted lines) and saltmarsh birds (solid lines). Bottom: boxplot of passage time for crossing transects at given distance marks from the spring staging site (500 km steps). Stars indicate a significant fixed effect of site in a mixed model for passage time with year and individual as random intercept effects

stores upon departure from the spring staging site partly determine reproductive success (Ebbinge, 1989).

Saltmarsh birds showed a delayed fuelling and departure relative to pasture birds. The advanced fuelling schedule of pasture birds allowed them to depart several days earlier, though this difference should be interpreted with care given the small sample size and overlap between the groups. Nonetheless, the difference in departure date may be important, because early arrival on the breeding grounds has been shown to be a critical fitness proxy in geese, related to improved breeding success (Prop, Black, & Shimmings, 2003). Eventually, close to the breeding grounds, the saltmarsh birds caught up timewise with the pasture birds, perhaps limiting any negative effects on reproductive success. However, in years with early snow melt in the Arctic, a scenario that is predicted to become more common (AMAP, 2017), earlier migration of pasture birds may represent a relative fitness benefit. Under an advancing spring, pastures currently provide more leeway for further advancement of migratory

schedules than saltmarshes, since plenty of high quality food is available on pastures even before the current start of migratory fuelling, when saltmarshes are still largely barren. It is therefore conceivable that the favourable pasture conditions during the entire spring season will draw in an increasing portion of the population in the future, leading to more conflicts between farming practices and geese.

Brent geese using the saltmarsh frequently foraged in the intertidal during low tide during the day. Intertidal forage has the potential to offset the otherwise more preferential conditions of pastures, because of its superior quality as a food resource, and potentially because of lower foraging costs. Intertidal food (algae, seagrass) had the highest overall quality, both in terms of a high nitrogen content and low fibre content. This high quality of intertidal plants is potentially induced by saline stressors to the plant (Fokkema et al., 2015), and because floating macroalgae and seagrass require less supportive tissue compared to terrestrial plants (Cyr & Pace, 1993). Intertidal food is more accessible to brent geese than to other herbivores because of their high salt tolerance (Stahl, Bos, & Loonen, 2002). Our tracking data also show a strong selection of intertidal habitats by brent in autumn and winter (both pasture and saltmarsh birds), with 79% of individuals overwintering in the intertidal of France and the UK (Fokkema et al., 2017).

The eastern Dutch Wadden Sea, in contrast to the western part, has seen slow recoveries of intertidal communities, including seagrasses (Dolch, Buschbaum, & Reise, 2013; Folmer et al., 2016), mussel beds, and general benthos hotspots (Compton et al., 2013). This spatial difference may explain why birds maintained a substantial intertidal lifestyle on the more eastern island of Schiermonnikoog, while at the pasture site of the more western island of Terschelling there was no clear evidence of foraging in the intertidal.

The saltmarsh on the island of Terschelling used to be a preferred area (Ebbinge, 1992), but is nowadays hardly being used anymore by brent geese. An additional explanation for the increased use of pastures may be that this saltmarsh has become older with taller vegetation. A saltmarsh is constantly subject to erosion and succession (Olff, De Leeuw, Bakker, Platerink, & Van Wijnen, 1997). Brent geese prefer the youngest parts of the saltmarsh, and can be evicted by ongoing succession (van der Wal, Lieshout, Bos, & Drent, 2000). Grazing by larger herbivores like hares and live stock keeps the saltmarsh in a younger state, and helps to keep it favourable for brent geese (Bos et al., 2005; van der Wal, van Wijnen, van Wieren, Beucher, & Bos, 2000).

We note that our sample size of tracked individuals was fairly small, which risks time budgets being biased by specifics of individuals. Time budgets and activity patterns are, however, very different for individuals on different habitats (Figure 1 top, middle), with little individual overlap between the two groups in the second half of the fuelling period (Figure 1 bottom). This suggests individual differences within sites are relatively small compared to between-site differences.

We further note that observational studies on free-living animals cannot explicitly address the causality in a chain of events. However, the alternative of experimentally manipulating each step is likely unfeasible and disruptive of the natural fuelling trajectories (Legagneux, Fast, Gauthier, & Bety, 2012), which we wanted to be representative for

the two habitat types as much as possible. The pasture management on Terschelling is comparable to dairy farming practices elsewhere in the Netherlands and north-western Europe (Thomassen, van Calker, Smits, Iepema, & de Boer, 2008), characterized by frequent application of manure and fertilizer. The marsh on Schiermonnikoog still actively expands to the east, and the successional gradient to very young stages makes it one of the most pristine saltmarshes of the Wadden Sea (Bos et al., 2005). Our pasture site can thus be considered fairly representative of farming practices elsewhere, while the saltmarsh is likely one of the higher quality marshes available to brent geese.

4.1 | Conservation and management implications

Based on historical hunting bags, brent geese population sizes are currently a fraction of the past (Ebbinge, 2014). 1930s wasting disease and subsequent eutrophication decimated seagrass populations in the northern hemisphere (Folmer et al., 2016; Godet et al., 2008). More locally, land reclamation works in the Netherlands deteriorated the growing conditions for intertidal food plants of brent geese (Eriksson et al., 2010). Brent geese remain a species of global concern subject to a multitude of risks: further intertidal habitat losses (Clausen & Clausen, 2014), degradation, succession, and eutrophication of remaining saltmarsh habitat (Ebbinge, 2014; van der Wal, Lieshout, et al., 2000; van der Wal, van Wijnen, et al., 2000), as well as climate-induced changes at the breeding sites, such as faltering lemming cycles (Nolet et al., 2013).

In this context, agricultural land has become an indispensable stopover habitat, and is likely to remain so in the foreseeable future. Birds depend here on policies and financial incentives for farmers, who allow birds to graze their land repeatedly. Such repeated grazing is essential for birds to keep grass in a young (short-sward) vegetative state (Bos et al., 2004). Financial incentives to farmers to let geese graze freely have brought disturbances at both our saltmarsh and pasture site to historically low levels, which is reflected in little time spent flying (down to 0.37 hr/day or less). This is considerably less than at an agricultural and saltmarsh sites in Denmark and the UK (Clausen, Clausen, Fox, Fælled, & Madsen, 2012; Riddington et al., 1996) (cf. factor 4 in Denmark), where disturbance-induced flying was identified as an important factor explaining habitat use. Ongoing losses of eelgrass and young saltmarsh habitat (Deegan et al., 2012; Ganter, 2000) make it unlikely that natural habitat alone can support current geese populations (Ebbinge, 1992). Without alternative natural habitat, brent currently remain dependent on low-disturbance pasture land, which however could be easily lost if farmers would resume active scaring should financial compensation cease (Bos & Stahl, 2003).

These historical and conservation contexts add weight to our current insight that sufficient availability of young saltmarsh and intertidal resources may be the most effective way for managers by which they can prevent brent geese from switching to agricultural pasture even further. Our comparative analysis suggests that geese on natural land may be living near a limit at which they reach a competitive disadvantage to birds fuelling on pasture sites. It is therefore critical that remaining saltmarsh habitat is not degraded any further.

Our study at a pristine saltmarsh suggests that saltmarsh management alone may be insufficient to prevent further habitat switching to pastures. Expanding the availability of nearby intertidal resources at saltmarshes is likely one of the most effective ways for keeping natural habitat attractive, because its food quality remains superior to terrestrial resources. The challenge for land managers is to create saltmarsh and intertidal conditions that allow brent geese to stick to their traditional niche, and thereby reduce the species' reliance on costly compensation schemes to farmers.

AUTHORS' CONTRIBUTIONS

A.D. performed the research and collected and analysed the data. W.F. coordinated field work on Schiermonnikoog, and collected and analysed saltmarsh and intertidal plant data. A.D. wrote the paper with input from B.N. and the other authors. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.j8cm402 (Dokter, Fokkema, Ebbinge, et al., 2018).

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SUPPORTING INFORMATION

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