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Does the Tundra Bean Goose (*Anser serrirostris*) Follow the Green Wave Throughout its Entire Spring Migration?

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HL, LF and LC conceived the idea and designed methodology. HL and LF collected the data. HL analyzed the data. HL led the writing of the manuscript, with contributions from LC. All authors contributed critically to the drafts.

Key words
***Anser serrirostris*, Eastern tundra bean goose, Spring migration, Green wave, Habitat use**

ABSTRACT

Following the flush of spring growth of primary production (the "green wave" hypothesis) has been applied as a universal explanation for spring migration timing of avian herbivores. However, studies of the green wave hypothesis have focused on species feeding intensively on above-ground primary production. To test whether a facultative grazer strictly follows the green wave, we used 16 complete tracks in time and space of spring migrating tundra bean geese (*Anser serrirostris*) fitted with telemetry devices from two flyways between Yangtze River Floodplain winter areas and Anadyr (Russia)/Central Arctic breeding grounds. We combined these with high spatial resolution MODIS satellite-derived plant production data to relate the timing of spring migration to that of the green wave index (GWI) at different staging regions and on breeding areas. Results showed that, at stopovers south of 52°N, eastern tundra bean geese fed mainly on cropland and arrived at stopover sites ahead of 50% GWI. At all subsequent stopover sites in Russia, eastern tundra bean geese fed exclusively on natural forage land, and followed GWI northwards, finally overtaking GWI to arrive at the breeding sites in advance of these dates. These data show that satellite-derived GWI are generally poor predictors of the arrival dates of spring migrating eastern tundra bean geese, but that deviations related to differential habitat use along the flyway and the need to arrive on the breeding areas ahead of snowmelt to coincide subsequent hatching of goslings with optimal food availability.

INTRODUCTION

Long-distance migratory wildfowl exploit patterns of seasonal resource availability in time and space throughout their annual cycle (Newton, 2008). Spring migration is very critical process especially for adult geese ready to breeding, as geese are assumed to be partial capital breeder, accumulating body store for breeding during spring migration (Drent *et al*., 2006). Therefore, selecting high-quality foraging sites during spring migration is critically important not only for successful migration and maximising lifetime fitness, but is the basis of reproductive success (Drent *et al*., 2006, Destin *et al*., 2009).

The green wave hypothesis assumes that following the flush of growth in above-ground primary production is considered to be a universal explanation for the timing of spring migration among avian herbivores (Van der Graaf *et al*., 2006; Shariatinajafabadi *et al*., 2014; Thorup *et al*., 2017). Satellite-derived MODIS normalized difference vegetation index (NDVI) offers a remote sensing means of measuring plant biomass, which can be used as a proxy of forage quality for herbivores (Skidmore and Ferwerda, 2008; Rivrud *et al*., 2016). Satellite-derived green wave index (GWI) transforms NDVI time series within each pixel into value between 0 and 100% to reflect changes in levels between the minimum and maximum NDVI measurements (Beck *et al*., 2008). Recent studies have indicated that GWI can accurately predict the timing of geese migration, since geese trade-off between forage quality and quantity to arrive at stopover sites close to the date of 50% GWI (i.e. at the assumed date of peak nitrogen concentration, Shariati Najafabadi *et al*., 2015).

Generally, studies of herbivore responses to the green wave have focused on species which specialise on feeding on net above-ground primary production, such as giant pandas (*Ailuropoda melanoleuca*) (Beck *et al*., 2008), mule deer (*Odocoileus hemionus*) (Merkle *et al*., 2016), barnacle geese (*Branta leucopsis*) (Shariatinajafabadi *et al*., 2014). In recent years, many migratory geese populations have shifted to feeding on agricultural surpluses left after the autumn harvest, which remain as field residues as profitable forage in the spring. Geese

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feeding on plant stems and farmland waste have no need to follow the green wave while gaining energetic benefits from exploiting such artificial resources, but to do so may lead to a mismatch between the timing of migration and the spring progress of the green wave.

To test whether a facultative grazer strictly follows the green wave, we utilize relatively high spatial resolution MODIS satellite-derived production data combined with spring detailed migration data from individually telemetry-tracked eastern tundra bean goose (*Anser serrirostris*). Arctic-nesting tundra bean goose intensively use cropland at stopover sites in China during spring migration (Si *et al.*, 2018). In contrast, during subsequent staging at uninhabited areas in Russia, they feed almost exclusively on natural habitats, unaffected by human land use change, where they likely subsist on above-ground primary production, where their timing of migration wold be expected to coincide with green up of vegetation. As a result, the eastern tundra bean goose is an ideal species to test the green wave hypothesis at different stages of its spring migration while staging in different regions and exploiting different habitats. We predict that the spring availability of residue corn in Northeast China remaining in snow free fields will enable eastern tundra bean geese to migrate to these areas to acquire body stores for onward migration before such fields are ploughed and drilled between the end of April and early May (Zhang and Hu, 2018), well ahead of the green wave. We predict that they will later catch the peak of forage quality in Russia where they utilize mainly natural habitats to accumulate sufficient body stores, but that ultimately they will jump ahead of the green wave to arrive at ultimate breeding areas in advance of primary production to coincide their breeding with optimal timing for gosling foraging.

MATERIALS AND METHODS

GPS tracking

We caught 48 tundra bean geese in Poyang from the Yangtze River Floodplain, Jiangxi Province, China (29.1°N, 115.9°E), and Anhui lakes (30.9°N, 117.6°E) during October 2016 and January 2017, using method described by Yu *et al.* (2017). We deployed GPS-GSM (Global Positioning System-Global System for Mobile Communications), solar-powered collar transmitters (Supplementary Table I) on captured individuals, ensuring that the weight of transmitter accounted for less than 2% of the bird body weight to minimize the effect of transmitter on birds (Demers *et al.*, 2003). These waterproofed devices collected transmitter ID, geographical coordinates (i.e. longitude, latitude (shown to have a horizontal accuracy of 9.6 ± 5.6 m SE in field tests)), velocity and timestamp of the GPS location. Finally, we acquired 16 completed spring tracks from 16 individuals, 4 of them migrate to Anadyr river (Russia) while 12 of them arrive to Central Arctic area (Fig. 1).

Fig. 1. Stopover sites, breeding areas and wintering areas from 16 migration tracks of bean geese. Different colours indicate different stay duration.

For each track we identified the stopover sites following the method of Wang *et al.* (2018). This method recognizes the changes in the movement pattern according to first passage time (FPT), a secondary signal of movement tracks (Edelhoff *et al*., 2016). FPT estimates the minimum crossing duration of an organism for a given radius along its path, which will be high when it resides within a restricted area, and low when it is travelling. We defined stopover sites as those where the geese stayed for at least two days (Drent *et al*., 2006; Kölzsch *et al*., 2015). Spring migration was defined from the time the geese left the last wintering site and reached breeding/prospecting site (Kölzsch *et al*., 2016).

Satellite-derived green wave index (GWI)

MODIS/Terra Vegetation Indices 16-Day 1 km products MOD13A2 Collection 6 (downloaded from https://lpdaac.usgs.gov) in 2017 were used to derive NDVI data used in the following analyses. To reduce the noise, we applied an adaptive Savitzky-Golay filter to produce smooth time series following the method of (Si *et al*., 2015). To obtain daily NDVI data, the 23 images obtained each year were linearly interpolated to daily images (Si *et al*., 2015; Shariati-Najafabadi *et al*., 2016). We calculated daily GWI for each pixel following the method of White *et* *al*. (1997) and Shariatinajafabadi *et al*. (2014):

$$GWI_t = (NDVI_t\text{-}NDVI_{min})/(NDVI_{max}\text{-}NDVI_{min}) \times 100\%$$

Where $NDVI_{min}$ and $NDVI_{max}$ are annual minimum and maximum NDVI values, while $NDVI_t$ and GWI_t are the NDVI and green wave index on date t. 0% GWI indicates the annual minimum NDVI and 100% GWI expresses the annual maximum NDVI. GWI data for stopover sites were extract from within united buffers of 10km around each fixed geese location. We masked water, forest, urban and built-up area, snow and ice, barren and sparsely vegetated, and unclassified areas from GWI map according to yearly global land cover products (MCD12Q1) downloaded from http://e4ftl01.cr.usgs.gov/MOLT/ (Si *et al*., 2015).

Habitat use

We first selected all possible feeding locations during the daytime (Zhang *et al*., 2018), and from these rejected positions assumed to be in flight (i.e. if the velocity >4m/s, Bengtsson *et al*., 2014). In the next step, we overlaid the feeding locations on GPS layers containing Finer Resolution Observation and Mornitoring-global land cover map 2017 with 30×30m resolution (Gong *et al*., 2019) to assign each location to a specific land cover type. The categories in the map are: “Cropland”, “Forest”, “Grassland”, “Shrubland”, “Wetland”, “Water”, “Tundra”, “Impervious surface”, “Bareland”, “Snow/Ice”. For the purpose of this analysis, we combined “Wetland”, “Grassland”, and “Tundra” as “Natural forage land”, “Cropland” as “Cropland”. For each staging region, we calculated the total percentage of position fixes within each category (Yu *et al*., 2017).

Relating satellite-derived green wave index to bean geese migration

We here assume that the timing of 50% GWI indicates the peak food availability for geese (Doiron *et al*., 2013) and defined the date when the GWI value most closely approximated to 50% GWI as the predicted arrival date of tundra bean geese. We calculated root-mean-square-deviation (RMSD) to assess the level of fitness between observed arrival date and predicted arrival date (i.e. date of 50% GWI), defining RMSD < 10 as good fitness, 10-15 as moderate, and >15 as poor, following Destin *et al*. (2009). The difference between the predicted and observed arrival date at stopover sites within different regions were tested using student *t*-tests. In addition, we fit linear model to assess the relationship between geese arrival date and predicted arrival date within the specific region.

RESULTS AND DISCUSSION

At stopover sites south of 52°N, the arrival date of Bean Geese was far earlier than the date of 50% GWI both for Anadyr (Russia) and Central Arctic geese (Supplementary Table II, Fig. 2). There were poor fits between predicted arrival date and observed arrival date. At stopover sites north of 52°N, the relationship between observed and predicted arrival date was strong for Central Arctic geese (slope = 0.67, R^2 = 0.49, p-value < 0.001). There were good fits between predicted and observed arrival date for Central Arctic geese. Only one Anadyr geese staged in Russia (for 7 days) and its arrival date was in advance of the date of 50% GWI (Supplementary Table II, Fig. 2). Both Anadyr and Central Arctic Geese arrived at breeding areas much earlier than the date of 50% GWI. The fit between predicted and observed arrival date of Central Arctic geese was better than that for Anadyr geese.

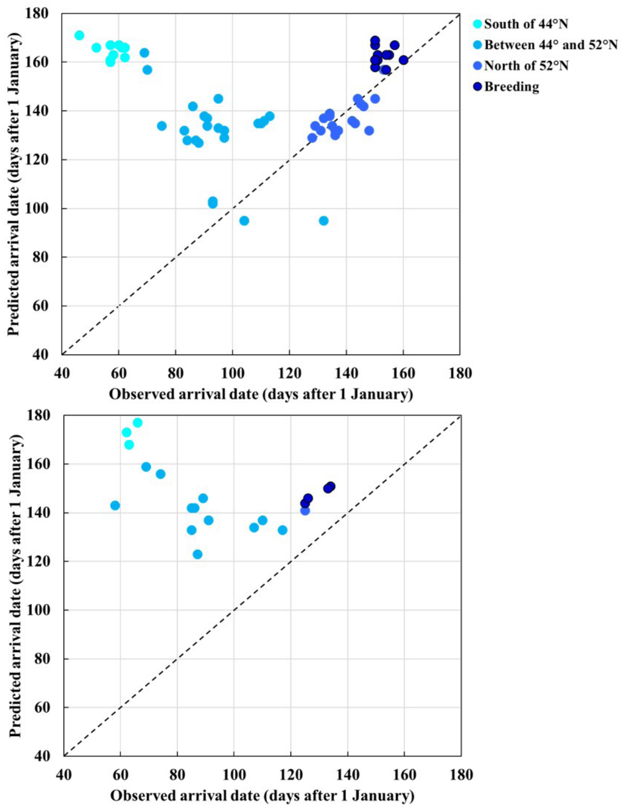

Fig. 2. The relationship between date of 50% GWI and observed arrival date at stopover sites during spring migration of Central Arctic (upper) and Anadyr (below) migration route. Different colors denote different regions.

Central Arctic geese used 37% of cropland at stopover sites south of 44°N and 34% croplands between 44° and 52°N (Fig. 3). Anadyr geese used 47% of cropland at stopover sites south of 44°N and 73% between 44° and 52°N, respectively (Fig. 3). In contrast, Central and Anadyr geese almost exclusively used natural forage habitats within Russia. GWI levels at stopover sites north of 52°N when geese stayed there was below 50%, compared to above 50% at stopover sites south of 52°N for Central Arctic geese (Fig. 3).

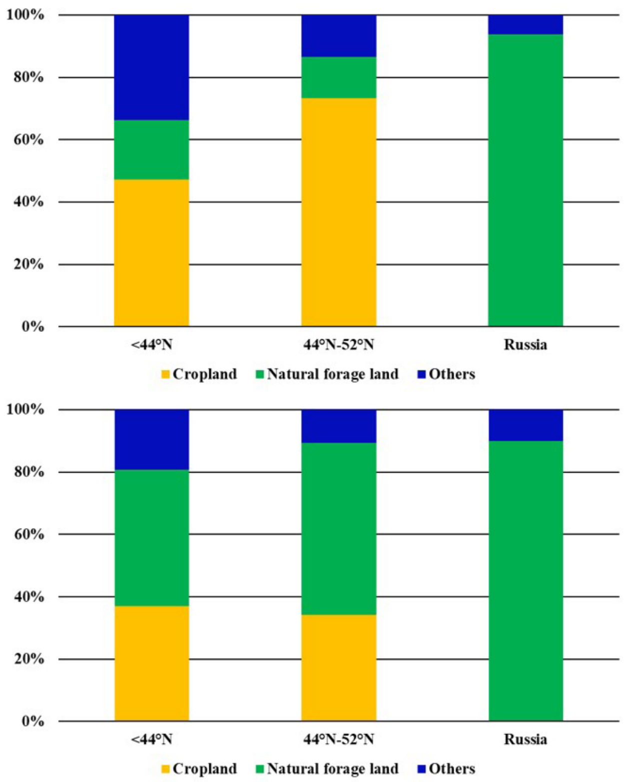

Fig. 3. Percentage of habitat use of tundra bean geese in three different spring staging regions of Anadyr geese (upper) and Central Arctic geese (below).

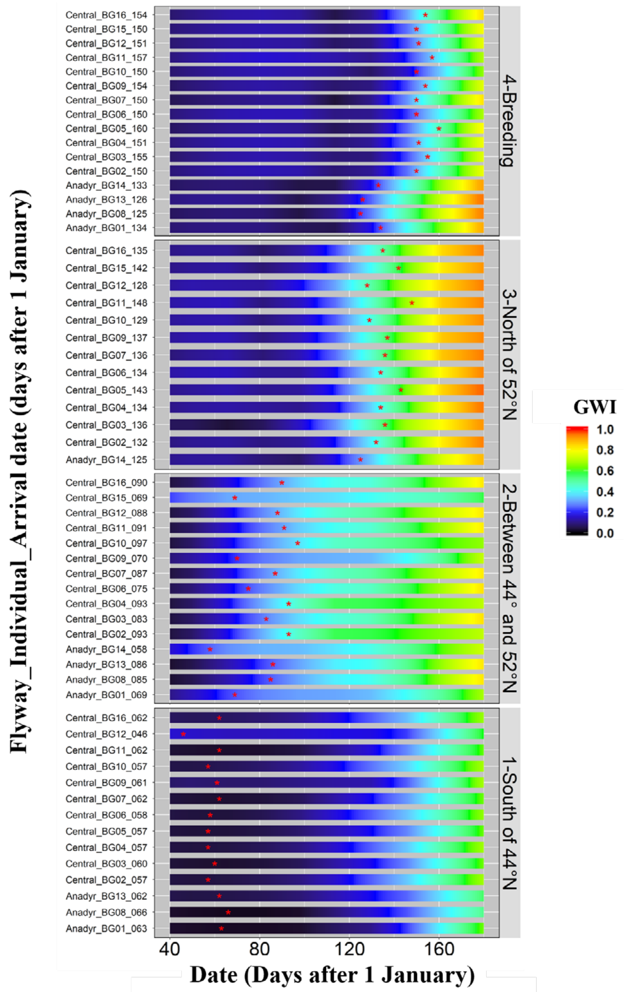

Fig. 4. Time line of GWI, arrival date (red stars) at staging regions visited by spring migratory tundra bean geese *Anser serrirostris* en route to the breeding areas in Anadyr (n = 4) and the Central Eurasian Arctic (n = 12).

Using relatively high spatiotemporal resolution satellite imagery combined with tracking data, we tested the green wave hypothesis along two flyways of Arctic nesting eastern tundra bean geese sympatrically wintering in China. Our results suggested that satellite-derived green wave index (GWI) could only partially predict the arrival date of eastern tundra bean geese during spring migration (Fig. 4) and it seems the deviations from the GWI were related to land use on the most southerly staging areas and the ultimate leap ahead of the GWI to arrive at breeding areas before the onset of plant growth. In stopovers within Russia, where geese almost exclusively exploited natural habitats, timing was more related to the GWI. South of 52°N, eastern tundra bean geese fed mainly on croplands and arrived at stopover sites far ahead of date of 50% GWI.

Tundra bean geese did not follow the green wave at stopover sites south of 52°N (i.e. mainly in Northeast China) during spring migration. Northeast China is a key area of commercial grain production in China (Yang *et al.*, 2007). Zhang *et al.* (2018) showed that tundra bean geese preferred croplands in China during spring migration, which is consistent with our findings (Figs. 3, Supplementary Fig. 1). Geese feed on crop residues left after machine harvesting, which enhances energy intake rates compared to natural foods and enables geese to accumulate energy more efficiently for migration and ultimately for breeding (Fox and Abraham, 2017). At the timing of geese staging in these areas, air temperatures are well below freezing point, as such primary production does not occur in such croplands when geese are present, hence crop waste is the only source of food and unrelated to the local GWI. The cultivation season in Northeast China is between end of April and early May (Zhang and Hu, 2018) while geese leave Northeast by early May, before the growth period of net above-ground primary production, which seems to result in a GWI below 50% when geese stay in stopover sites south of 52°N (Fig. 3) so that geese have no chance to pursue the 50% GWI. Although Central Arctic geese use more than 40% of natural forage land at staging sites between 44°and 52°N, the growth period in Inner Mongolia plateau is between May and October (Jin *et al*., 2009), after the geese leave, which also causes the low level of GWI when geese stay there (Supplementary Fig. 2) and later date of peak of food availability (Supplementary Fig. 2).

Another reason causing the mismatch between spring migration and green wave may be human disturbance. Geese suffer from wide-scale hunting and poisoning by poachers in China (Roller MaMing, 2012), which confined five wintering geese into natural wetland, avoiding human activity. Tundra bean geese fly directly from Yangtze river to Northeast China during spring migration with no stopover (Fig. 1). They seem to avoid high population density region (which often means high human activity), according to the spatial pattern of population density from Sun *et al*. (2016). They may also miss the chance to follow the green wave because of the long-distance jump. Geese in Europe migrated in short legs than geese in China (Wang *et al*., 2018), they may have higher flexibility to adapt their migration to green wave.

This study supports that geese arrive at breeding area before the peak of food availability. Geese from both flyways arrive at breeding area before 50% GWI, which enable gosling to benefit from the longer period of high food quality (Drent *et al*., 2006, Xu and Si, 2019). Moreover, early arrival in the breeding area can enable them to reduce competition by occupying territory with advantage (Kokko, 1999).

Although we should be prudent about concluding so much from so few tracked individuals within only one season, the similar pattern between arrival date and the date of 50% GWI from two flyways is further confirmation that the green wave hypothesis is not the universal explanation for the timing of migratory movements in herbivorous wildfowl. The use of habitat, and in particular the shifts between crop waste and above ground primary production, is likely the most important factor that determines whether organisms follow the peak in quality of primary production along the spring migration corridor. This study also indicates that the management of cropland is critically important for the conservation of herbivorous wildfowl, because these geese now rely upon the availability of crop waste to acquire energy and nutrient stores to fuel onward migration over inhospitable terrain (Wang *et al*., 2018). These stores also bridge the resource shortage experienced by the Anadyr nesting geese, which migrate from Northeast China to breeding area without stopover (Fig. 1). Geese from two flyways both use high rate of cropland, and show a mismatch with the peak of food availability that would potentially occur if they were reliant on above ground green growth. Because the geese have modified their migration in time and space to become reliant upon an artificial source of food in Northeast China, they are now vulnerable to changes in land use in these areas. Future conservation plans to safeguard these migratory waterbird populations therefore need to take account of such changes in habitat use if they are to maintain these populations for future generations.

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Supplementary material

There is supplementary material associated with this article. Access the material online at: https://dx.doi.org/10.17582/journal.pjz/20190502130556

Statement of conflict of interest

The author declares that they have no conflict of interests.

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