Migratory herbivorous waterfowl couple the seed wave and the green wave during spring migration

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Abstract

Since the 1950s, many wetlands in China have been transformed into farmlands. In response, East Asian waterfowl populations have taken advantage of spilled seeds left after harvest and now intensively use farmlands during migration. Accordingly, waterfowl might have expanded their migration strategy from merely surfing the green wave of newly emerging vegetation to also incorporating post-harvest agricultural seeds for refueling en route. However, how migratory birds use the phenology of multiple food resources to time their seasonal migration is yet to be explored. Here, we use 166 spring migration tracks of five East Asian herbivorous waterfowl species with a mixed-effect resource selection function model to test how waterfowl use the newly emerging vegetation (the green wave) and the post-harvest agricultural seeds (the seed wave) during spring migration. We find waterfowl arrive at their core stopover sites in the Northeast China Plain after agricultural seeds become available and extend their stay after spring vegetation emerges. Smaller-bodied species tend to arrive at this area later to better use the newly emerged vegetation. Regarding the breeding site, four geese species arrive after the emergence of vegetation, while tundra swans are slightly earlier. Our findings suggest that a strategy of resource coupling has allowed waterfowl to cope with the environmental change that has occurred along their migration routes: they time their migration to exploit both natural and anthropogenic food resources. Management initiatives that combine the preservation of natural habitats with adaptive agricultural practices could safeguard these threatened, long-distance migratory bird species.

Significance Statement

East Asia is experiencing human-induced climate and habitat change at an alarming rate, impacting migratory birds. Conservation challenges largely depend on the cues used by migratory birds to track resources. For the first time, we test a migration strategy of coupling the phenology of natural and anthropogenic food resources, which act in combination to shape the spring migration phenology of herbivorous waterfowl. Waterfowl use both resources by arriving at core stopover sites after seeds become available on farmland and extend their stay after spring vegetation emerges. The exact timing varies among species, with smaller-bodied species, preferring for newly emerging vegetation, arriving later. These findings advance our understanding of migration mechanisms, which will inform and guide effective management and conservation efforts.

Main Text

Introduction

Migratory species move between their breeding and non-breeding grounds and benefit from the exploitation of seasonal food resources across the annual cycle. Foraging opportunities occur in a series of pulses, at different times and places, which generate "resource waves" across the landscape (1-4). The green wave hypothesis posits that the migration progress of herbivores is driven by the seasonal growth of new vegetation at stopover sites along the migration route (5, 6). This hypothesis has been verified in a variety of herbivorous animal groups, such as geese (3, 5, 7-9) and ungulates (10-12), according to individual-level information compiled using tracking technology (5) to population-level information compiled by large-scale community science initiatives (13). During northward migration, birds mainly arrive at their stopover sites after the emergence of spring vegetation, but can reach their breeding grounds earlier, thus overtaking the green wave, and allowing their offspring to benefit from the peaks of food resources (3, 8). While herbivorous species have been documented to track the green wave in Northern Europe (5, 9, 14) and North America (13), this has not been the case for many herbivorous waterfowl populations worldwide, especially within East Asia (14).

Due to extensive land cover change worldwide, herbivorous waterfowl have expanded from using natural ecosystems to exploiting food resources in agricultural landscapes (15, 16). For example, during the spring-staging period, migratory herbivorous waterfowl have been observed to consume new sown cereals in Europe (17) and post-harvest corn remaining in cornfields (18) and spilled grain in rice paddies (19, 20) in North America. This way they benefit from the spread and post-harvest management of agricultural lands (21, 22). Since the 1950s, large areas of wetland in China have been converted into farmlands (23-26). East Asian waterfowl populations have started to take advantage of the spilled seeds left after harvest and now intensively use farmlands (27), especially in their core stopover area, the Northeast China Plain (28, 29). As a consequence, the green wave hypothesis (3, 5), generated mainly based on the spatio-temporal dynamics of the natural habitats, does not fully encapsulate the migration strategy adopted by East Asian waterfowl.

Migratory herbivorous waterfowl use the natural habitat (e.g., wetlands, grasslands, shrublands) and farmland habitat differently. Since many waterbodies and grasslands in East Asia are semi-natural, we use the term ‘natural habitat’ hereafter to represent areas where birds feed on spring sprouts of vegetation. Within farmlands, East Asian waterfowl primarily consume seeds, rather than crop vegetation, e.g., spilled grains and leftover maize (Fig. 1*B*) that remain after harvest (29). These items have been found to offer a higher food quality compared to natural vegetation (15). Spilled seeds on farmland are not available all year round, but only after the harvest during the previous fall and during the time that the ground is not frozen (i.e., during the winter this resource is not accessible). However, how herbivorous waterfowl exploit seeds when they become available

(the seed wave) in relation to how they take advantage of the emergence of new vegetation (the green wave) during migration is yet to be explored.

We hypothesize that migratory herbivorous waterfowl could take advantage of the phenology of both seed wave (i.e., seed availability in farmlands using the end of snowmelt as a surrogate; Fig. 1*B*) and green wave (i.e., newly emerged vegetation in natural habitats; Fig. 1*C*) during spring migration (Fig. 1*A*). We present 166 spring migration tracks from 2015 to 2021, derived from satellite tracking of 99 individuals for five herbivorous waterfowl species (swan goose *Anser cygnoides*, tundra bean goose *A. serrirostris*, greater white-fronted goose *A. albifrons*, lesser white-fronted goose *A. erythropus*, and tundra swan *Cygnus columbianus*) in East Asia. Using a mixed-effect resource selection function model, we analyze whether birds time their migration to couple the seed wave and the green wave during spring migration. Investigating how herbivorous waterfowl track the spatiotemporal availability of these widely different food resources allows furthering our understanding of migration mechanisms, predicting the impact of land cover and climate change on migratory birds, and guiding effective habitat management for migratory bird conservation.

Results

We analyze the relationship between spatiotemporal bird migration patterns (*SI Appendix,* Table S1 and Fig. S1) and the availability of two food resources (i.e., seeds and newly emerged vegetation). Spring migration tracks (n = 166) from 2015 to 2021 of five waterfowl species within the East Asian – Australasian Flyway are used: 22 tracks of swan geese, 8 of tundra swans, 54 of tundra bean geese, 62 of greater white-fronted geese, and 20 of lesser white-fronted geese. Seed resources at farmlands are all distributed below 55°N latitude (*SI Appendix,* Fig. S2). Tracked birds utilize both natural habitats (water and surrounding wetlands, grassland, and shrublands) and farmlands (especially in the Northeast China Plain). In Russia (above 55°N latitude), waterfowl mainly use water, shrublands, grasslands, and wetlands. They briefly stay at wetlands or rivers that occurred within forests, which explains the high proportion of forest habitats used in this region (*SI Appendix,* Fig. S2*F-H*). At breeding sites, tracked birds use grasslands, wetlands, and shrublands as major habitats (*SI Appendix,* Fig. S2).

Herbivorous waterfowl in East Asia adopt a strategy in which they couple the seed wave with the green wave during spring migration (Fig. 2 and Fig. 3). Observed arrival timings of all study species match the period that seeds become available (using the end of snowmelt as a surrogate) within their core stopover area, the Northeast China Plain, before new vegetation become available (Fig. 2, *SI Appendix,* Fig. S3 and Fig. S4). Across all study species, birds arrive at the core stopover sites in the Northeast China Plain in early April (96 ± 14 Julian days, Fig. 2). The period when seeds become available in this region is at the end of March, whereas the emergence of new vegetation

occurs around early May. Waterfowl depart from the Northeast China Plain region in mid-May (131 ± 12 Julian days, Fig. 2). In the Russian stopover sites, the observed arrival timings primarily match the end of snowmelt (around the end of May and the beginning of June). Birds reach their breeding sites after onset of vegetation growth (around early June) (*SI Appendix,* Fig. S4 and Table S1).

The strategy of coupling the two types of food resources, seeds and newly emerged plants, varies among species (Fig. 2 and Fig. 3). For arctic-breeding species, those with a relatively larger body size (i.e., tundra swans and tundra bean geese) show a relatively earlier departure from the wintering sites ($F = 16.14$, $P < 0.001$, *SI Appendix,* Table S1), and a relatively earlier arrival on the Northeast China Plain ($F = 40.04$, $P < 0.001$, Fig. 3*A, C, E, and G* and *SI Appendix,* Table S1) and breeding sites ($F = 7.79$, $P < 0.001$, Fig. 3*B, D, F, and H* and *SI Appendix,* Table S1), in comparison to those smaller-bodied species (i.e., greater white-fronted geese and lesser white-fronted geese). Tundra swans arrive at the Northeast China Plain soon (i.e., only one day) after the snow melts and seeds become accessible (Table 1; Fig. 3*A*), whereas smaller-bodied goose species arrive later, after seeds have already become available for almost one week (for tundra bean geese; Fig. 3*C*) or for three weeks (for greater white-fronted geese and lesser white-fronted geese; Fig. 3*E and G*). All arctic-breeding species extend their stay at the Northeast China Plain to be able to forage on newly emerged plants (Fig. 2).

On the breeding grounds, three arctic-breeding goose species (i.e., tundra bean geese, greater white-fronted geese, and lesser white-fronted geese) arrive at their breeding sites after the plant emergence (Table 1, Fig. 3*D*, *F*, and *H*), whereas tundra swans arrive at the breeding sites relatively earlier, soon after the onset of snowmelt (Table 1, Fig. 3*B*). Mid-latitude breeding swan geese depart from the wintering site during mid-March (*SI Appendix,* Table S1) and arrive at the Northeast China Plain and the breeding sites around three weeks after the local onset of vegetation growth (Table 1, Fig. 3*I* and *J*). They spend a larger percentage of time on farmlands before mid-April, and then mainly use natural food resource later in the season (*SI Appendix,* Fig. S3).

Discussion

We discover a spring migration strategy used by East Asian herbivorous waterfowl in which they couple the ‘seed wave’ of seed accessibility on farmland with the ‘green wave’ of newly emerging vegetation in natural habitat. All study species arrive at their core stopover sites in the Northeast China Plain after the start of seed availability on farmlands, extend their stay to use newly emerged vegetation, and arrive at the breeding sites after the emergence of spring vegetation. Only tundra swans arrive at the breeding grounds earlier, after the onset of snowmelt. This strategy in which migration is timed to be able to take advantage of both natural and anthropogenic food resources

allows East Asian herbivorous waterfowl to exploit the vast and variable landscapes along their migration routes.

East Asian herbivorous waterfowl time their staging in the core stopover sites Northeast China Plain to make use of both anthropogenic and natural food resources. Seeds leftover from previous year's harvest on the unfrozen ground (i.e., the beginning of April) and newly emerged plants (i.e., in early May) allow migratory birds to replenish their energy for an extended period of time during stopover, which facilitates arriving at the breeding grounds in an optimal condition. The Northeast China Plain contains 15% of the total farming area in China, with maize, soybean, and rice being the three major crop types (30). Crop seeds on farmlands could provide a high-nutrient food source for herbivorous waterfowl, especially during early spring, when snow just starts melting and food in their natural habitats is insufficient. Management of agricultural lands has had a great impact on how birds use seeds. The seed-availability period in the Northeast China Plain ends with the start of sowing, at the end of April (31) (*SI Appendix,* Fig. S5). Mechanical ploughing (*SI Appendix,* Fig. S5*A*) at the end of April predicts sowing (*SI Appendix,* Fig. S5*B* and *C*). In early May, seeds covered with pesticides are sowed (*SI Appendix,* Fig. S5*C*), which means crop seeds on farmlands are no longer useable for waterfowl (field observations and personal communications with local farmers; *SI Appendix,* Fig. S5). When seeds are not available anymore, all study species are able to forage on newly emerged plants in natural habitats, and depart from the Northeast China Plain in mid-May.

Although all study species arrive at the core stopover sites after the seed wave and depart after the spring vegetation emergence, their exact migration timing differs. Arctic breeders (i.e., tundra swans, tundra bean geese, greater white-fronted geese, and lesser white-fronted geese) arrive at the Northeast China Plain stopover sites after the start of seed availability and before new vegetation emerges. The departure date from the wintering sites is later for smaller-bodied species. The largest-bodied tundra swans leave the earliest and the smallest-bodied lesser white-fronted geese leave the latest (*SI Appendix,* Table S1), suggesting body size is of importance for migration strategy. One explanation could be that smaller-bodied grazing species, namely the greater and lesser white-fronted geese, depart later from the wintering site (*SI Appendix,* Table S1), so that they can forage on newly emerging grasses in their wintering ground (32-34). By arriving later in the stopover areas, they could also make use of the new spring vegetation for a longer period. Larger-bodied herbivorous waterfowl, namely tundra swans and tundra bean geese, generally are less sensitive to forage quality, and therefore can utilize relatively more diverse assortment of food resources (33, 35).

Tundra swans prefer open water where underwater food resources can be easily accessed (e.g., tubers and algae) that, just like seeds, only become accessible after snowmelt (36). They arrive the earliest at their core stopover sites (soon after seeds and underwater food become available),

and also move on towards their breeding sites the earliest. Tundra bean geese arrive at the Northeast China Plain only one week after seeds have become available. In contrast, mid-latitude breeding swan geese only arrive at the core stopover sites after the emergence of vegetation. This probably reflects that swan geese could easily get access to nutrient-rich food and reach their destination under relatively warm weather conditions (37). According to our findings, East Asian herbivorous waterfowl species we studied take species-dependent utilization of food resources temporally, though they share similar spatial distributions in the Northeast China Plain. This likely explains how the species can coexist in the same landscape.

All study species arrive at their breeding sites after the onset of vegetation growth and close to the end of snowmelt, except for tundra swans, which arrive relatively earlier. This is probably because larger-bodied arctic-breeders generally invest more time on breeding activities and face a more time-constrained window in which they have to lay eggs, molt, and raise chicks, than smaller-bodied species and mid-latitude breeders (3, 38, 39). The slower pace in their life-histories (i.e., laying larger eggs with a longer incubation and gosling-rearing period) drives birds to reach the breeding grounds earlier and lay eggs earlier (39). This is particularly the case for tundra swans, with the largest body size among the five herbivorous waterfowl, which overtake the green wave, but can use underwater food resources once the ice melts (36). The three smaller-bodied species arrive at the arctic later, after vegetation has newly emerged, and close to the end of snowmelt. This is in line with a previous study reporting that East Asian geese follow the retreating snow northwards and arrive at their arctic breeding sites prior to the end of snowmelt (40). We find geese couple the use of seeds and newly emerged vegetation as they move north to enable accumulating sufficient fuel during migration, and avoiding to arrive so early that they deplete their body stores prior to the local thaw, therewith ensuring that their goslings benefit from abundant food resources later in the season (3, 5, 40).

Mid-latitude breeding swan geese reach their breeding grounds after spring vegetation emergence and around two weeks after the end of snowmelt (i.e., around late April and early May). The growing season in Inner Mongolia (i.e., breeding grounds for swan geese) typically lasts six months from May to October (41). This long breeding window makes swan geese less time-constrained than arctic-breeding species. Swan geese specialize on submerged tubers, which are only available when lakes have melted, although both field observations and our tracking data suggest swan geese can graze on sedges and grass (42, 43). A former study observed that swan geese breeding in Eastern Mongolia (i.e., the same population as our study species) take significantly longer periods to arrive at their breeding grounds than those breeding in Central or Western Mongolian, due to a prolonged staging at the core stopover sites in the Northeast China Plain (44). Their arrival on the breeding grounds coincides with the date that minimum temperatures are above the freezing point of water (44).

Climate change might induce shifts in vegetation phenology in the spring (45-47), thereby changing food availability for herbivorous waterfowl at a different pace at different sites (48). A reduced predictability of food supply due to phenological asynchrony would be exacerbated when different food resources are coupled. As a consequence, species may struggle to advance their migration timing to match food availability (49). Even though some goose species can accelerate their migration speed under global warming, they might still suffer population declines if they cannot store sufficient nutrients for egg-laying (38). For species taking advantages of the seed wave, migration timing and pace could be influenced by changes in cultivation practices. For example, changes in farming calendars might affect seed availability (16, 28). Different responses to environmental change between the timing of cultivation and bird migration phenology might cause ecological traps and population declines of migratory birds (50, 51). Therefore, changes in habitat management should consider conservation needs, especially for species that have been forced to depend on human-dominated landscapes (52).

Our study offers the first empirical evidence that birds couple both phenology of anthropogenic and natural food resources in migration. Specifically, we document that anthropogenic and natural factors act in combination to shape the spring migration phenology of herbivorous waterfowl. We recommend the resource coupling strategy is further tested in additional species and within different flyways. To what extent populations of migratory herbivorous waterfowl benefit or suffer from this coupling strategy needs to be thoroughly investigated. For example, how the seed wave itself is affected by climate and habitat change, is still unknown. A proper understanding of the impact of global environmental change and different human cultivating activities on migratory bird species will inform and guide effective habitat management for migratory bird conservation worldwide.

Materials and Methods

Analyzing bird migration patterns

We analyzed the satellite tracking data of five East Asian herbivorous waterfowl species. Lesser white-fronted geese (*Anser erythropus*), greater white-fronted geese (*A. albifrons*), tundra bean geese (*A. serrirostris*), and tundra swans (*Cygnus columbianus*) were captured and tagged at their East Dongting Lake (29°N, 113°E) and Poyang Lake (29°N, 116°E) wintering sites in the Yangtze River Floodplain, China during the 2014 to 2018 wintering seasons. Swan geese (*A. cygnoides*) were captured at the breeding site Hulun Lake, Hulun Buir, China (48.3°N, 117.4°E) during the 2017 molting season. All birds were equipped with GPS - GSM (Global Positioning System – Global System for Mobile Communications), solar-powered loggers. GPS locations were recorded every 2 h. Information used in the analysis on migration patterns include Bird ID, track year, longitude,

latitude, and time of the GPS location. Detailed methods on birds capture and deployment of the satellite transmitters can be found in Si*, et al.* (29) and Lei*, et al.* (27).

Migration parameters (*SI Appendix,* Table S1) were derived from 166 spring migration tracks of five species from 2015 to 2021, covering 22 tracks of swan geese from 19 individuals, 8 of tundra swans from 4 individuals, 54 of tundra bean geese from 28 individuals, 62 of greater white-fronted geese from 34 individuals, and 20 of lesser white-fronted geese from 14 individuals. All tracking data of five species are stored in Movebank (www.movebank.org), under ID 731644623 for lesser white-fronted geese, 1614083125 for greater white-fronted geese, 1614098614 for tundra bean geese, 1614096661 for swan geese, and 1614102131 for tundra swans. For each track, we labeled daytime and nighttime locations, by identifying the sunrise and sunset time for each location based on algorithms provided by the National Oceanic & Atmospheric Administration (NOAA) (https://www.esrl.noaa.gov/) (35). The spring migration period, defined as GPS locations recorded from the day that birds left their wintering sites to the day that they reached their breeding sites (7), was included in the analysis. Stopover sites and the length of stay in each site were identified through the space-time permutation model in the SaTScan statistics (http://www.satscan.org) (29). We defined the stopover sites as those sites where birds stayed for at least two days and moved within a radius of less than 50 km (29, 53). The arrival/departure time of the wintering/stopover/breeding sites for each individual in each track year were defined as the first day it arrived/left a specific site in which it showed a continuous presence/absence for at least three days (28). Differences on the migration timing across species were assessed using one-way ANOVA followed by Tukey's honestly significant difference (HSD) multiple comparison. Cumulative length of stay in the Northeast China Plain and Russian stopover sites was defined as the sum of all days spent at stopover sites by an individual in its respective region. Migration distance was defined as the cumulative distance travelled between the wintering site and breeding site (29).

Investigating habitat use along the spring migration route

To examine the habitat use of tracked birds along the migration route, we used two land cover products. The 30 m spatial resolution spring land cover product from 2015 (54) was selected to capture the natural habitats and farmlands within China. The European Space Agency Climate Change Initiative (ESA-CCI) 300 m spatial resolution land cover product from 2015 (http://maps.elie.ucl.ac.be/CCI/viewer/index.php) was used to capture the relatively homogeneous landscape within Russia. Two classification systems from the two products were aggregated into seven land cover types: grassland, farmland, water, wetland, forest, shrubland, and ‘other’ (i.e., barren land, lichens and mosses, snow and ice, or impervious). Habitat use at each stopover site was estimated using the percentage of bird GPS locations on each land cover type (29). The relative proportion of land cover types in use at each latitude was then calculated as the sum of the

percentage of bird GPS locations on each land cover type across all stopover sites (their rounded centroid coordinates) located within the same latitudinal range. As waterfowl mostly forage during the day, we also calculated the habitat use at daytime (i.e., the proportion of land cover in use during the day) across the whole spring migration period, to better interpret how waterfowl use the food resources across time.

Calculating the timing of the seed wave and the green wave

For each track, the spring vegetation emergence time in natural habitats and the start of seed availability time on farmlands were calculated. We used the second-order derivative (55, 56) of the smoothed time series of Enhanced Vegetation Index (EVI) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) Terra 8-day 250 m spatial resolution surface reflectance product MOD09Q1 to extract the spring vegetation emergence time (details are provided in *SI Appendix*, SI methods S1). Only pure pixels where the proportion of herbaceous area (i.e., wetlands, grasslands, and shrublands) was larger than 0.5 within a 250 m grid cell were used (details are provided in *SI Appendix*, SI methods S2 and Fig. S6).

The start of the seed availability time was determined by the end of snowmelt in spring because after the snow melt seeds (remaining from previous year's harvest) could be easily dug out from the ground. Following the method of Rickbeil*, et al.* (57), we used the MODIS Terra Snow Cover daily 500 m spatial resolution product MOD10A1 to measure the different degree of snowmelt (i.e., the onset and the end of snowmelt). We first created a time-series to capture the daily percent of snow cover (from day 1 to day 210) for each stopover and breeding site, for each track. We then applied three-piece segmented regression to extract the onset and the end of snowmelt for each pixel (*SI Appendix,* Fig. S7). To facilitate interpreting the resource use, in addition to the vegetation availability date and the seed availability date, we also calculated the onset of snowmelt and the end of snowmelt at each site, for each individual bird, in each track year.

Determining the resource availability – bird arrival relationship

We used a resource selection function (RSF) framework (58, 59) to investigate to what extent the start of resource availability can be matched with the arrival date at the stopover or breeding sites for migratory herbivorous waterfowl during spring migration. Using a logistic regression of presence/absence points, RSFs can be used to define the selection of resources on the day when waterfowl arrive at a specific site (28). The presence points were defined as all GPS locations recorded on the day of arrival. The absence points were drawn randomly on the date before and after arrival at a specific site during the spring migration period. For each pixel in the specific site, we calculated the number of days between each of the four indices (i.e., the spring vegetation emergence, the start of seed availability, the onset of snowmelt, and the end of snowmelt) and the

bird arrival date. Migratory waterfowl might not track the exact day that a specific resource becomes available but may display a lag effect, where birds arrive before (positive lag value) or after (negative lag value) the resource becomes available (14). In order to obtain the focal lag (i.e., the number of days before or after the resource available or snow melt dates), we tested the predictive ability of the models across a series of temporal lags, by adding or subtracting days to the resource becoming available or the snow melt dates, following (59). For example, if a bird arrives at the stopover site two days after seed availability, the model with a lag of two (by subtracting two from the day to the seed availability date) would have the highest likelihood.

We executed RSFs in two regions for each species: the core stopover area Northeast China Plain and the breeding sites. We ran two models in the Northeast China Plain stopover sites (35°-55°N latitude) using vegetation and seed availability as the predictors, and three both at the mid-latitude (around 46°-49°N latitude) and arctic breeding sites (around 70°-75°N latitude) using vegetation availability, the onset of snowmelt, and the end of snowmelt as predictors. For each of the five waterfowl species, within each region, we fit a mixed effects conditional logistic regression model using a binomial distribution as the link function. The response variable was the probability of bird arrival. The presence was set to 1 and absence was set to 0. The fixed effect for each model was a specific type of temporal lag, i.e., lag days to 1) the spring vegetation emergence, 2) the start of seed availability, 3) the onset of snowmelt, or 4) the end of snowmelt. The random effect was the identity of the individual track (track ID). We used the R package glmmTMB to run the analysis (60).

We modelled the lags in days to food availability or the snow melt conditions that fell between the 10th and 90th percentile of all locations within each region used by herbivorous waterfowl. We selected the top model for the focal lag based on the lowest Akaike Information Criterion (AIC) (59). The range around the optimal lag was also estimated by predicting the day at which interpolated log-likelihood values have a difference of 1 (ΔAIC = 2). The difference in range was then calculated by the number of days between the minimum and maximum estimate. The predictive performance of the top models with the optimal estimated lag was evaluated by k-fold cross-validation (59, 61).

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Figures and Tables

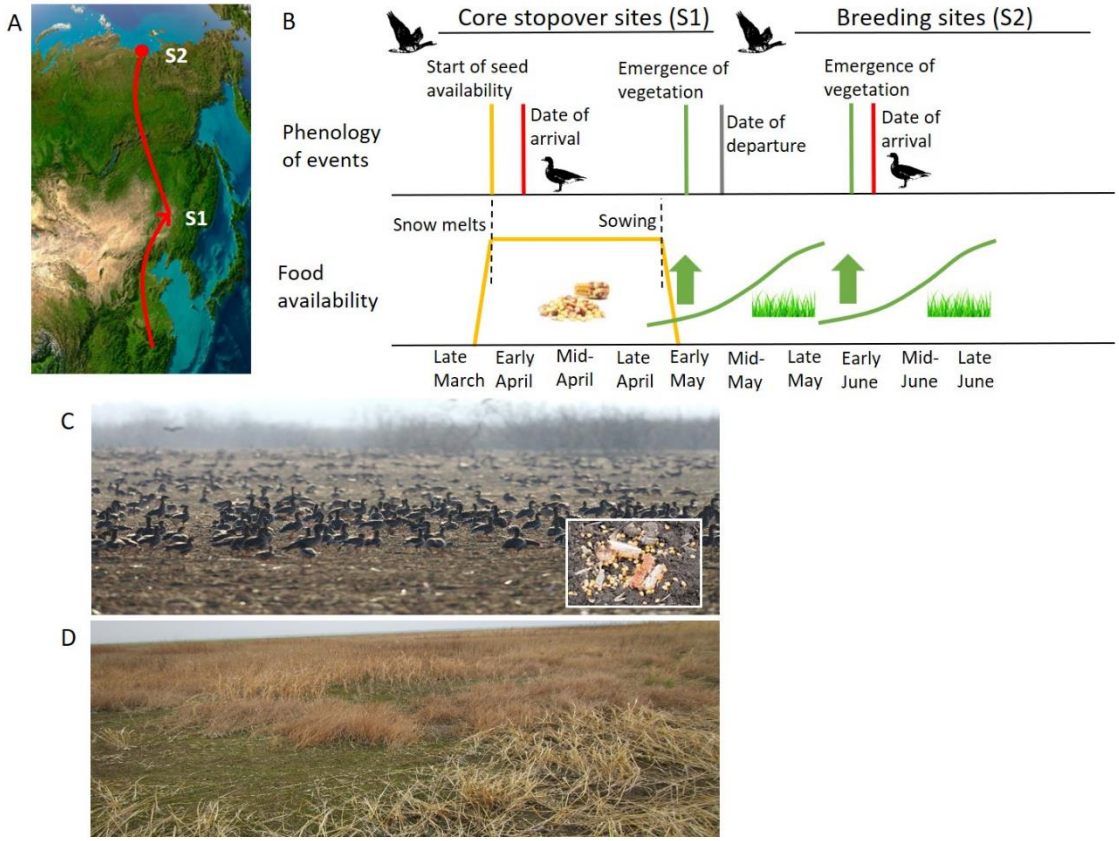

Figure 1. Schematic diagram of the newly discovered spring migration strategy adopted by East Asian migratory herbivorous waterfowl in which they couple two food resources. (A) Core stopover sites (S1) and breeding sites (S2) along the spring migration route. (B) During spring migration, birds arrive on farmlands at the core stopover sites after the start of seed availability (seed wave; orange line), extend their stay after spring vegetation in natural habitats emerges (green wave; green lines) (S1) and reach the breeding grounds after the emergence of vegetation (green wave; green lines) (S2). (C) Photo of greater white-fronted geese (*Anser albifrons*) and tundra bean geese (*A. serrirostris*) foraging in farmlands (taken 19 March 2021) on Yuquan island, Hunchun, Yanbian Korean Nationality Autonomous Prefecture, Jilin, China (photo credit: Haixiang Zhou). Inset photo shows leftover maize (taken 2 May 2016) on farmlands in Fuyu Village, Nehe, Qiqihar, China (photo credit: Jie Wei). (D) Photo of new spring vegetation (taken 1 May 2016) embedded in old vegetation in Baishan town, Longjiang, Qiqihar, China (photo credit: Jie Wei).

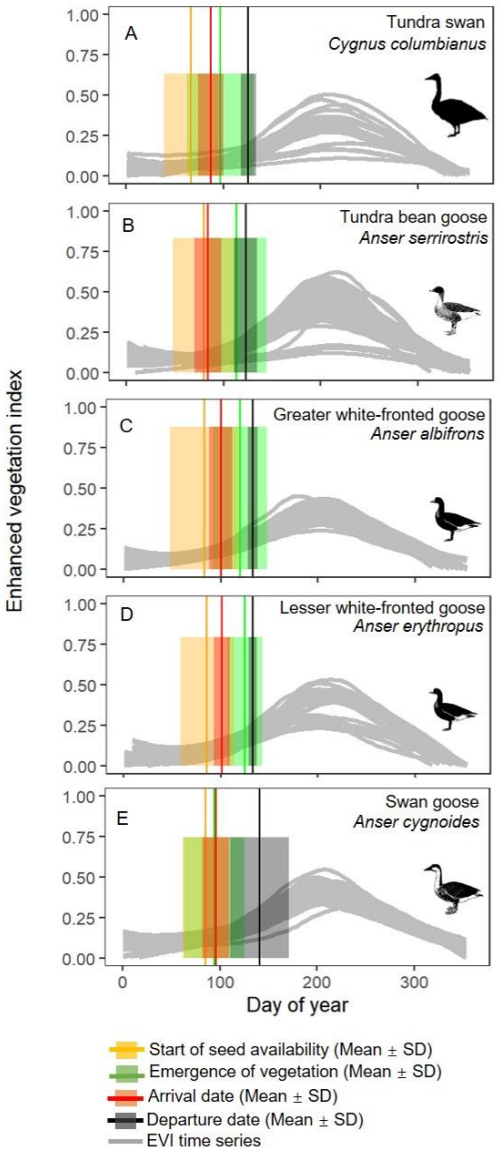

Figure 2. Coupling the seed and green wave at core stopover sites in the Northeast China Plain. All study species (A-E) arrive (vertical red line with error bar) at the Northeast China Plain after the start of seed availability (vertical orange line with error bar) and departed (vertical black line with error bar) from this region after the emergence of vegetation (vertical green line with error bar), thereby use both food resources. Grey lines show annual food availability indicated by enhanced vegetation index (EVI) time series.

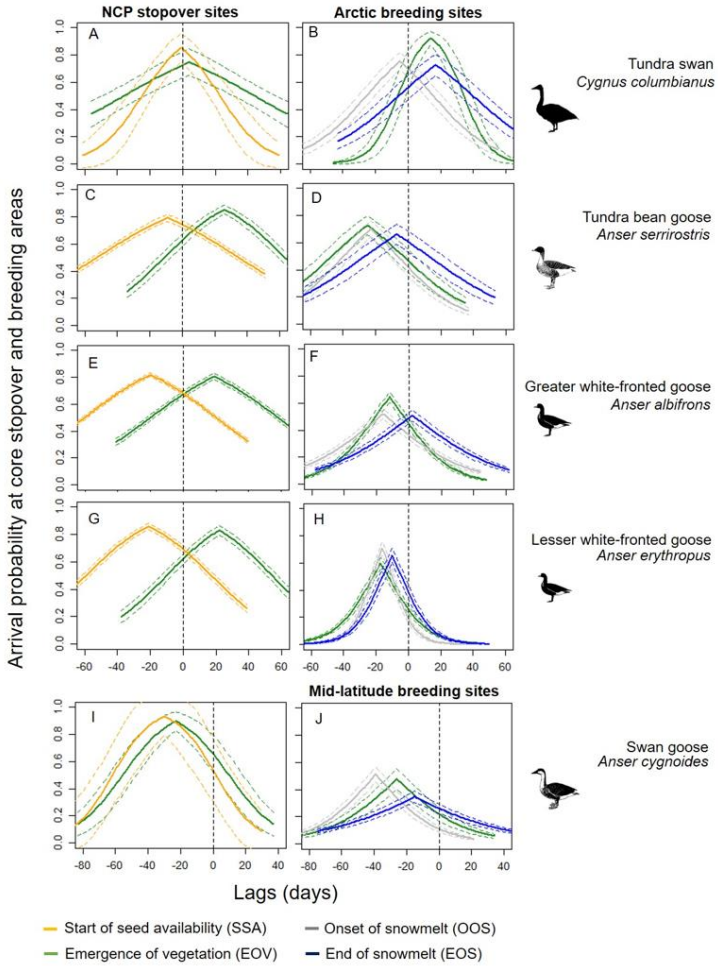

Figure 3. Arrival probability in relation to the availability of seeds and newly emerged vegetation for East Asian migratory herbivorous waterfowl during spring migration. The highest arrival probability for arctic-breeding birds occurred after the start of seed availability (SSA; orange lines) and before the emergence of vegetation (EOV; green lines) in the Northeast China Plain (NCP) stopover sites (A, C, E, G). All arctic-breeding geese reached their breeding sites after the emergence of vegetation (EOV in D, F, H; green lines) and close to the end of snowmelt (EOS in D, F, H; blue lines). Tundra swans arrived at the arctic breeding ground earlier (after the onset of snowmelt; OOS in B; grey lines). Mid-latitude breeding swan geese (I, J) reached the Northeast China Plain and the breeding sites after the emergence of vegetation (EOV; green lines). Colored dashed lines represent 95% confidence intervals. Vertical dashed lines represent the bird arrival date. Lags (x axis) indicate the lag days in comparison to the timing of resource availability or the timing of snowmelt.

Table 1. The top resource selection models showing the estimated optimal lags (days) on resource availability and snowmelt conditions for five East Asian herbivorous waterfowl species at core stopover sites the Northeast China Plain and the breeding sites.

Region	Species	Models	Estimated days with range	Difference	Log-likelihood	K-fold scores	
						Mean	SE
Northeast China Plain	Tundra swan	Plant *	4 (-3.4, 13.7)	17.1	-213.57	0.427	0.450
		Seed †	-1 (-5.5, 4.8)	10.3	-24.10	0.571	0.169
	Tundra bean goose	Plant	26 (24.3, 27.8)	3.5	-101.14	0.873	0.125
		Seed	-9 (-11.1, -5.9)	5.2	-42.04	0.503	0.143
	Greater white-fronted goose	Plant	19 (17.7, 21.7)	4	-1522.14	0.935	0.025
		Seed	-20 (-20.7, -18.9)	1.8	-4067.08	0.394	0.278
	Lesser white-fronted goose	Plant	22 (20.2, 24.2)	4	-466.73	0.914	0.014
		Seed	-21 (-22.2, -19.9)	2.3	-1398.77	0.358	0.053
	Swan goose	Plant	-23 (-25.1, -19.5)	5.6	-1107.01	0.403	0.397
		Seed	-30 (-35.7, -20.6)	15.1	-1380.99	0.487	0.546
Breeding sites	Tundra swan	Plant	14 (12.9, 16)	3.1	-6198.94	0.530	0.130
		Onset of snowmelt	-5 (-6.6, -2.3)	4.3	-5916.80	0.417	0.451
		End of snowmelt	17 (16.1, 17.4)	1.3	-6789.48	0.523	0.108
	Tundra bean goose	Plant	-25 (-26, -23.5)	2.5	-336.80	0.301	0.164
		Onset of snowmelt	-23 (-23.4, -21.6)	1.8	-484.11	0.253	0.165
		End of snowmelt	-7 (-9.5, -4.7)	4.8	-514.02	0.572	0.152
	Greater white-fronted goose	Plant	-12 (-12.2, -11)	1.2	-6332.97	0.628	0.182
		Onset of snowmelt	-16 (-17.1, -15.6)	1.5	-7455.17	0.434	0.081
		End of snowmelt	2 (0.5, 3.1)	2.6	-7569.63	0.859	0.093
	Lesser white-fronted goose	Plant	-17 (-17.8, -16.9)	0.9	-2464.9	0.406	0.140
		Onset of snowmelt	-16 (-16.9, -15.9)	1	-1999.08	0.384	0.082
		End of snowmelt	-10 (-10.1, -9.9)	0.2	-2171.43	0.648	0.128
	Swan goose	Plant	-26 (-26.3, -25.8)	0.5	-3562.83	0.595	0.340
		Onset of snowmelt	-39 (-39.7, -37.7)	2	-3449.32	0.312	0.730
		End of snowmelt	-15 (-16, -14.4)	1.6	-3785.92	0.466	0.242

* The model using the spring vegetation emergence as a predictor

† The model using the start of seed availability as a predictor