Land use change and the migration geography of Greater White-fronted geese in European Russia

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Abstract. Large areas of agricultural land have been abandoned in European Russia since 1991, triggering succession toward more wooded landscapes, especially in northern regions where conditions for agriculture are more challenging. We hypothesize that this process has contributed to a southward shift by migratory Atlantic Greater White-fronted geese, as stopover sites in northern Russia became progressively less suitable. To test this hypothesis, we located stopover sites from information contained in 2976 ring recoveries and sightings of neck-collared geese. These records were divided into three time periods, chosen to reflect major changes in the economy and land use of European Russia: 1960–1990, 1991–2000, and 2001–2013. We used a kernel density estimator grid to delineate areas surrounding 300 putative stopover sites, and statistically evaluated the effects of latitude, distance to nearest waterbody, settlement, and period on stopover site usage by geese. Our results show that over the three periods, usage of the stopover sites has shifted southward, indicating that Greater White-fronted geese have shifted their migration pathway, with the greatest shift in the most recent period. This shift was confirmed by a highly significant squared latitude term and significant interaction term between periods. The nearest settlements showed no significant effect on stopover site usage while the nearest waterbody term was negative, suggesting higher waterbody densities contributed to higher densities of stopover sites. We attribute the shift to the successful reforestation of the Russian landscape that has followed widespread land abandonment, especially that following the break-up of the former USSR.

Key words: agriculture; geese migration; land use change; political ecology; Russia; stopover sites.

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INTRODUCTION

Every year, geese migrate between wintering grounds in Western Europe and breeding areas in northern Russia. Most goose species are typical avian migrants and spend most of their migration period at stopover sites, where they rest and refuel (Schaub et al. 2001, Kölzs ch et al. 2016). Hedenström and Alerstam (1997) estimate the ratio of time at stopover sites to time in flight for a typical small migratory bird at about 7:1, and this ratio is even higher for larger birds like geese (Klaassen et al. 2006, Eichhorn et al. 2009). Greater White-fronted geese Anser albifrons are the most numerous of all goose species using the East Atlantic flyway: The current population is estimated at 1.3 M individuals (Fox et al. 2010, Koffijberg and van Winden 2014). Atlantic Greater White-fronted geese concentrate their wintering time in northwestern Europe (Mooij...
They breed on the Russian tundra, ranging from Kolguev Island (Kondratyev and Kruckenberg 2013) up to the Taymyr Peninsula (Mooij 1997). Spring migration takes them in a northeasterly direction, initially on a narrow front, but fanning out over a widening front across Poland, Lithuania, Belarus, Ukraine, and European Russia (Polakowski et al. 2018), and narrowing again toward breeding areas in the Russian Arctic (Madsen et al. 1999). The pattern in the fall is similar, as geese return from the north over almost all of European Russia north of 50° N (Madsen et al. 1999, Emelchenko 2009). A second population of Greater White-fronted geese overwinters on the Hungarian plains (Farago 2010). Their migration route lies south of Belgorod and north of the Danube Delta, the Sea of Azov, and the Volga Delta (Mooij 1997, Emelchenko 2009). Individual geese are known to move between these flyways (Mooij et al. 1996; B. Nolet, personal communication). Stopover sites for Greater White-fronted geese are found across this vast area of ~4 McKm². During the past 40 yr, the study of goose migration has increased both on the seaboards of the North Sea (Arzel et al. 2006) and the Russian Arctic Ocean (Arzel et al. 2006, Emelchenko 2009), but the stopover sites outside the area of the European Union have received relatively little attention (Jankowiak et al. 2015, Kölzsch et al. 2016). The likely reasons are limited accessibility due to the poor conditions of Russian country roads especially during spring (thaw) and autumn (rain), the vastness of the lands, political isolation precluding visits by foreign ornithologists, and a dearth of Russian scientists studying bird migration. Stopover sites may also have received less attention from ecologists due to the influence of theories on migrant population regulation that stress food limitation (Lack 1956) on either wintering (Drent and Prins 1987, Drent and van der Wal 1998) or breeding areas (Cooke et al. 1983, Jefferies and Rockwell 2002). Improving relations between the West and Russia allowed a series of expeditions to the Taymyr Peninsula (Russia) to test these ideas (Kostin and Mooij 1995, Mooij et al. 1996, Ebbinge et al. 2013). Attention began to turn to migration as a possibly limiting period as it became clear that neither breeding- nor wintering-limitation hypotheses worked well to explain population regulation (Ebbinge 1985, Drent et al. 2006).

An ideal spring stopover site (sensu Zimin et al. 2002, Drent et al. 2006, Si et al. 2011) for Greater White-fronted geese is characterized by (1) the proximity of a fresh water body of minimally 20 ha and maximally up to several thousand km², such as found at the shore waters of Lakes Ladoga, Onega, and Ilmen (58° N–60° N), which provide good sites for staging geese, and (2) open fields consisting of grasslands (shorter than 7 cm: Heuermann et al. 2011, Si et al. 2011, Zhang et al. 2015), meadows and pastures (Zhao et al. 2012, Polakowski and Kasprzykowski 2016), cereals (wheat, barley, oats, rye), stubbles (Nilsson and Persson 2000, Rosin et al. 2012), or potato and sugar beet leftovers from the previous harvest (Ely and Raveling 2011). Hence, many stopover sites are located on agricultural land and were created or modified by people.

After the break-up of the USSR in 1991, there was a sweeping reorganization of agriculture in the parts of European Russia visited by Atlantic Greater White-fronted geese (M. Grishchenko, H. H. H. T. Prins, M. E. Schaepman, W. F. de Boer, R. C. Ydenberg, and H. J. de Knegt, unpublished manuscript). Vast areas of agricultural land were abandoned because it was not economically profitable to maintain agriculture after subsidized collective farming came to an end (Wegren 1995). Land abandonment in this eco-climatic zone mostly leads to old-field succession and forest regeneration (Kuemmerle et al. 2015) that we hypothesize has negatively impacted the abundance and quality of stopover sites. Further, as landscape changes in Russian declining agriculture started in the economic periphery (i.e., the north; Grishchenko and Prins 2016) and spread toward the south (Ioffe and Nefedova 2004), we hypothesize that a coincident shift in the distribution of stopover sites occurred. We predict that in the decades following the break-up of the USSR, Greater White-fronted geese shifted their utilization of stopover sites in European Russia southward.

METHODS

Stopover locations

Our study aimed to identify stopover sites in European Russia over which Atlantic Greater White-fronted Geese migrate between their...
wintering areas in northwestern European (The Netherlands, Germany) and breeding areas in the Russian Arctic (from Kola Peninsula to the Lena Delta). We excluded wintering and breeding areas from the analyses. The study area includes all the provinces of European Russia (Table 1) with the exception of Nenets Autonomous Okrug, which is located in the tundra zone and contains geese breeding areas.

We located stopover sites based on sites used by migrating Greater White-fronted geese. First, from metal rings (of geese ringed in The

Table 1. List of provinces in European Russia from which goose data were retrieved.

| Province                | Federal District | Number of recoveries | Capital     | Area, km² |
|-------------------------|------------------|----------------------|-------------|-----------|
| Belgorod Oblast         | Central          | 35                   | Belgorod    | 27,000    |
| Bryansk Oblast          | Central          | 12                   | Bryansk     | 35,000    |
| Vladimir Oblast         | Central          | 26                   | Vladimir    | 29,000    |
| Voronezh Oblast         | Central          | 13                   | Voronezh    | 52,000    |
| Ivanovo Oblast          | Central          | 39                   | Ivanovo     | 21,000    |
| Kaluga Oblast           | Central          | 9                    | Kaluga      | 30,000    |
| Kostroma Oblast         | Central          | 1159                 | Kostroma    | 60,000    |
| Kursk Oblast            | Central          | 13                   | Kursk       | 30,000    |
| Lipetsk Oblast          | Central          | 22                   | Lipetsk     | 24,000    |
| Moscow Oblast           | Central          | 95                   | Moscow      | 44,000    |
| Oryol Oblast            | Central          | 5                    | Oryol       | 25,000    |
| Ryazan Oblast           | Central          | 166                  | Ryazan      | 40,000    |
| Smolensk Oblast         | Central          | 13                   | Smolensk    | 50,000    |
| Tambov Oblast           | Central          | 22                   | Tambov      | 34,000    |
| Tver Oblast             | Central          | 93                   | Tver        | 84,000    |
| Tula Oblast             | Central          | 26                   | Tula        | 26,000    |
| Yaroslavl Oblast        | Central          | 100                  | Yaroslavl   | 36,000    |
| Republic of Karelia     | Northwestern     | 572                  | Petrozavodsk| 181,000  |
| Republic of Komi        | Northwestern     | 45                   | Syktyvkar   | 417,000   |
| Arkhangelsk Oblast      | Northwestern     | 383                  | Arkhangelsk | 590,000   |
| Vologda Oblast          | Northwestern     | 117                  | Vologda     | 145,000   |
| Kaliningrad Oblast      | Northwestern     | 21                   | Kaliningrad | 15,000    |
| Leningrad Oblast        | Northwestern     | 70                   | Saint Petersburg | 84,000 |
| Murmansk Oblast         | Northwestern     | 12                   | Murmansk    | 145,000   |
| Novgorod Oblast         | Northwestern     | 93                   | Veliky Novgorod | 55,000  |
| Pskov Oblast            | Northwestern     | 24                   | Pskov       | 55,000    |
| Perm Krai               | Volga            | 2                    | Perm        | 160,000   |
| Republic of Bashkortostan| Volga           | 2                    | Ufa         | 143,000   |
| Republic of Mary El     | Volga            | 9                    | Joshkar-Ola | 23,000    |
| Republic of Mordovia    | Volga            | 15                   | Saransk     | 26,000    |
| Republic of Tatarstan   | Volga            | 22                   | Kazan       | 68,000    |
| Republic of Udmurtiya   | Volga            | 7                    | Izhevsk     | 42,000    |
| Chuvash Republic        | Volga            | 6                    | Cheboksary  | 18,000    |
| Kirov Oblast            | Volga            | 47                   | Kirov       | 120,000   |
| Nizhny Novgorod Oblast  | Volga            | 37                   | Nizhny Novgorod | 77,000  |
| Orenburg Oblast         | Volga            | 6                    | Orenburg    | 124,000   |
| Penza Oblast            | Volga            | 9                    | Penza       | 43,000    |
| Samara Oblast           | Volga            | 8                    | Samara      | 54,000    |
| Saratov Oblast          | Volga            | 9                    | Saratov     | 101,000   |
| Ulyanovsk Oblast        | Volga            | 7                    | Ulyanovsk   | 37,000    |
| Krasnodar Krai          | Southern         | 4                    | Krasnodar   | 75,000    |
| Astrakhan Oblast        | Southern         | 1                    | Astrakhan   | 49,000    |
| Volgograd Oblast        | Southern         | 9                    | Volgograd   | 113,000   |
| Stavropol Krai          | North Caucasus   | 1                    | Stavropol   | 66,000    |
| Total: 45               |                 | 5                    |             | 3,673,000 |

Note: Total number of recoveries for each province is reported.
Netherlands during 1960–2013) returned or reported to the Vogeltrekstation Nederland, we identified the geographical locations at which 901 Greater White-fronted geese were shot in Russia. Goose hunters in Russia use shotguns, which are lethal only at short distances, and we surmise that these kills were made close to or at stopover sites. A second source of data was 2075 visual observations of Greater White-fronted geese wearing colored and numbered neck collars fitted in The Netherlands (95%) or northwest Germany (5%) in 1990–2013. These geese were sighted by volunteer observers and reported via www.geese.org. Both metal ring and neck-collar data were sourced through www.geese.org, a joint initiative of the Dutch organizations Alterra, SOVON, and NIOO (B. S. Ebbinge, unpublished data). Each record contained the ring or collar number, geographical coordinates of ringing and recovery sites, date and time of ringing, and the date and time of recovery. The recovery of an individual metal ring is unique to an individual goose and yielded a single record (when the goose was shot). Individual neck collars could potentially contribute multiple resightings. Of these, we included the location of the first observation of an individual in each year. Subsequent observations of an individual bird in that year were included only if located at least 7.5 km distant from the previous record. This threshold was determined by analyzing the spatial distribution of nearest-neighbor distances between stopover sites known prior to this analysis. The distribution of nearest-neighbor distances between stopover sites of Greater White-fronted geese is depicted in Fig. 1.

Fig. 1. Distance between nearest-neighbor stopover sites of Atlantic Greater white-fronted Geese in European Russia 1990–2013, based on recoveries of metal rings from shot birds, and sightings of birds with neck collars.
Sample sizes are summarized in Table 2. Totals of 2075 neck-collar sightings (410 duplicate records removed) and 901 metal rings (total \( n = 2976 \)) were divided into three time periods, chosen to reflect major changes in the economy and land use of European Russia (M. Grishchenko, H. H. T. Prins, M. E. Schaepman, W. F. de Boer, R. C. Ydenberg, and H. J. de Knecht, unpublished manuscript). These are period 1 (1960–1990; before the dissolution of the USSR) with 366 records, period 2 (1991–2000; period of economic transition) with 381 records, and period 3 (2001–2013; period of economic growth) with 2229 records.

### Spatial analysis

Stopover sites were located by calculating a kernel density estimator (KDE) grid for all the ring recovery and neck-collar resighting locations. When individual geese had several records, equal weight was assigned to each. Based on the output KDE surface, the center of a grid cell was scored as a stopover site centroid if the grid cell’s KDE value was equal to the maximum value in its 5 × 5 grid-cell neighborhood centered on the focal site.

To delineate the area corresponding to each stopover site, we partitioned the space using a Voronoi tessellation based on the stopover site centroids (Du et al. 1999). Large polygons represent stopover sites with low stopover site density, whereas small polygons are found in areas with a high density of stopover sites. The KDE value for each stopover site represents the number of associated records. We calculated the area of each polygon using ArcGIS tools (ESRI 2016), and to account for differences in stopover site density between three study periods also computed the area relative to the mean polygon size for that period.

### Results

To test whether migration pathways have shifted southward over time, we regressed the relative density of stopover sites (a measure of the amount of stopover use) in relation to latitude, for each period. We used the inverse of the relative area as a proxy for the spatial density of stopover sites. Stopover sites are generally located close to appropriate waterbodies and in areas modified by agriculture (i.e., close to main human settlements), so co-variates (distance to nearest waterbody, distance to nearest human settlement) were included in the model to account for potential confounds with the latitudinal pattern generated by the spatial distribution of waterbodies and agriculture. Both were log_{10}-transformed to better fit the assumptions of regression analysis. Latitude was represented with linear as well as quadratic terms to capture non-linearity in the relation of stopover site density to the latitudinal gradient. We used this standard technique because we expected a curved response shape with an intermediate peak. We included period (treated as a categorical variable; p1, p2, p3) as well as the interaction between period and latitude. We performed all regression analyses in R Studio (R version 3.3.2, R Core Team 2016).

### Table 2. Number of metal ring and neck collars reported from European Russia for Atlantic Greater white-fronted geese in three periods: period 1, 1960–1990; period 2, 1991–2000; and period 3, 2001–2013.

| Period   | Metal rings | Neck collars | Total   | Number of polygons |
|----------|-------------|--------------|---------|--------------------|
| Period 1 | 319         | 47           | 366     | 200                |
| Period 2 | 212         | 169          | 381     | 158                |
| Period 3 | 370         | 1859         | 2229    | 295                |

Note: The concept and utility of polygons are explained in the Methods section.
nearest waterbody was negative, indicating that proximity to a waterbody increased the density of stopover sites. The interaction term (latitude by period) was significant, with the period 3 (2001–2013) effect largest. Fig. 4 depicts the interaction, showing a progressive southward shift in the maximum density of stopover usage from period 1 through period 3 (from 1960 through 2013). The shift was most pronounced in period 3. The predicted relative densities for all three periods intersect at a latitude of about 58° N, where the majority of metal rings and neck collars were recovered, and hence, the relative density of stopover sites is highest.
DISCUSSION

Our results support the prediction that compared with the period between 1960 and 1990, migrating Greater White-fronted geese have progressively shifted their use of stopover sites in European Russia southward. This is consistent with our hypothesis that the ongoing abandonment of agricultural land in the northern parts of European Russia is leading to a loss of suitable stopover sites as forests regenerate and shrublands increase in cover.

Flexibility in migration has been recorded in many other avian species. Sutherland (1998) cataloged 43 cases of marked change in migratory patterns and notes that such changes must often have been made in evolutionary history in response to changes in climate, vegetation zones or sea level. He posed the question of whether migratory populations will be able to adapt to the accelerating rate of change of the global environment. The scale and pace of the migratory adjustments described here are therefore of interest.

Fig. 3. Space tessellation of the study area in European Russia during three observational periods (period 1, 1960–1990; period 2, 1991–2000; and period 3, 2001–2013).

Table 3. Multiple regression analysis (F6, 646 = 24.99, $P < 0.001$, adjusted $r^2 = 0.18$) with the relative density of stopover sites as response variable and as predictors: latitude, distance to settlement, distance to water, and the interaction of latitude and period.

| Factor                                    | b     | SE   | P-value |
|-------------------------------------------|-------|------|---------|
| Latitude                                  | -0.0115 | 0.0178 | N.S.    |
| Latitude$^2$                              | -0.0185 | 0.0020 | <0.001  |
| In distance to settlement                 | -0.0644 | 0.0699 | N.S.    |
| In distance to water                      | -0.1359 | 0.0425 | <0.01   |
| Latitude: 1991–2000                       | -0.0158 | 0.0275 | N.S.    |
| Latitude: 2001–2013                       | -0.0742 | 0.0237 | <0.01   |

Notes: SE, standard error. Distances were log$_{10}$-transformed prior to analyses. To remove correlation between the linear and squared term for the predictor latitude, we centered the predictor to zero mean by subtracting the mean latitude of ~58° N.
We attribute the southward shift to old-field succession leading to bush encroachment and reforestation, especially across the northern part of the country. This successional change led to a decline in the suitability of many locations as stopover sites, as they changed from open croplands to shrublands and eventually forest. This process has resulted from changes in the practice of agriculture in European Russia. As described by M. Grishchenko M., H. H. T. Prins, M. E. Schaepman, W. F. de Boer, R. C. Ydenberg, and H. J. de Knegt (unpublished manuscript), forest clearance in Russia reached its maximum extent coincident with the 1917 revolution. Since that time, a variety of processes have reduced the area devoted to pasture and crops and allowed fields to return to their natural cover (i.e., forest in northern regions). For example, farming rapidly mechanized in Russia after WW I, greatly reducing the extensive area required to pasture and grow food for the 30 M horses that had powered agriculture in 1918. This process accelerated after the break-up of the USSR in 1991. Many agricultural activities ceased, and large-scale abandonment of fields (Prishchepov et al. 2013) and agricultural communities began in the economic periphery of the north and spread toward central Russia (Ioffe and Nefedova 2004). The successional process requires 15 yr or longer for enclosed stands of trees recognizable as forests to develop, but fields become unsuitable as stopover sites for geese in as little as three years after abandonment (Grishchenko and Prins 2016). Longer and more mature grass is less desirable as food (Drent et al. 2006, Heuermann et al. 2011), and shrubbery provides cover for predators that geese perceive as dangerous (Jonker et al. 2010). Higher forest cover and diminishing intensity of agricultural activities (Jankowiak et al. 2015) decrease suitability of roosting areas for migrating geese. In contrast to northern areas, agriculture has remained

Fig. 4. Log relative density (inverse of relative area) of observed (points) and predicted (lines) stopover sites as function of latitude during three observational periods (period 1: black, 1960–1990; period 2: red, 1991–2000; and period 3: green, 2001–2013). Relative densities increase over time at lower latitudes, yet decrease over time at higher latitudes, thus indicating a southward shift of stopover sites. The southward shift is about 5°.
profitable in the south of Russia, where a variety of crops are cultivated that in other regions, geese find attractive (e.g., winter wheat, potatoes, sugar beets).

Another possible explanation for the observed shift lies in altered hunting patterns in Russia. The Greater White-fronted goose is a game species in Russia, and an estimated 10–30% of the entire population is shot annually across Europe (Kokko et al. 1998; B. S. Ebbinge, personal communication). Geese are well-known to be sensitive to hunting pressure (Fox and Madsen 1997), and readily move to safer areas in response (Fox and Madsen 1997, Jankowiak et al. 2015). For example, in spring Pink-footed Geese Anser brachyrhynchus move to Belgium when the hunting is opened further north, that is, in The Netherlands (E. Kuijken, personal communication). The safer stopover sites can be found in the vicinity of protected areas, for example, important bird areas (IBA), or in areas or countries where hunting is not permitted, at least during the migration (e.g., Natura 2000 areas; Jankowiak et al. 2015). However, most hunters in Russia live in areas with high human population density, that is, in the south and in the center around Moscow (Ioffe and Nefedova 2004, Braden 2014). Therefore, geese should have shifted their migration to the north, and not to the south, if they had responded to increased hunting pressure.

Sutherland (1998) listed global climate change as a likely cause of migration route change, and it has been explicitly considered as the reason for recent changes in the migration patterns of other goose species (Van Wijk et al. 2012). It is therefore a possible alternative explanation for the shift we documented here. Geese follow, at least in a broad sense (Si et al. 2015), a green wave of new growth northward in spring (Ydenberg and Prins 1981, Drent et al. 2006). By advancing phenology, this process could influence the timing and routing of goose migration. Earlier departure from wintering grounds and earlier arrival to stopover and breeding areas might confirm such emerging pattern (Eichhorn et al. 2009, van Wijk et al. 2012). However, these effects are not confirmed at stopover sites used by Greater White-fronted geese (Polakowski et al. 2018).

Climate change could also lead to changes in vegetation phenology. For example, temperatures have been increasing in sub-polar areas where the majority of geese breed (Bauer et al. 2008, Fox et al. 2010). Generally, global warming would lead to a northerly shift of biome boundaries, moving both the tree line and the steppe-forest boundary northward. Hence, climate change is expected to contribute to a shift in goose migration northward, which is opposite to the direction documented here. This conclusion is similar to that reached by Jonker et al. (2010) in their analysis of the reasons for the changed timing of barnacle goose migration. They rejected the influence of climate change on the green wave as an explanation, because it would have changed timing in the direction opposite to that observed.

In recent decades, the number of eagles has increased throughout Europe, and the authors (M. Grishchenko and H. H. T. Prins) observed large numbers of White-tailed eagles (Haliaeetus albicilla) on the major rivers in Russia along the southern extent of the Greater White-fronted goose migration. The recovery of the White-tailed eagle in the Baltic Sea has strongly influenced the migration and spring staging of Barnacle geese that winter in The Netherlands (Jonker et al. 2010), and it seems plausible that a similar process underlies changes in Greater White-fronted goose migration. A southward shift in their migration might be somehow a response to increased numbers of large birds of prey, in particular the White-tailed eagle. This would serve another possible explanation of the shift. Unfortunately, information is as yet too sparse for a good evaluation of this possibility.

In this paper, we tested a hypothesis if Greater White-fronted geese have been shifting their migration path as a response to growing land abandonment, especially in northern European Russia. By examining resightings from metal rings and neckbands across European Russia over the last 40 yr, we detected a progressive southward shift, matching in pace and direction changes in agricultural practice across European Russia over the past four decades.

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