esa ECOSPHERE

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

Mikhail Grishchenko,[1,†] Herbert H. T. Prins,[1] Ronald C. Ydenberg,[1,2] Michael E. Schaepman,[3] Willem F. de Boer,[1] and Henrik J. de Knegt[1]

[1]*Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3, Wageningen, 6708PB The Netherlands*
[2]*Biological Sciences, Simon Fraser University, 8888 University Road, Burnaby, British Columbia V5A 1S6 778 782 4282 Canada*
[3]*Department of Geography, University of Zurich, Winterthurerstrasse 190, Zürich 8057 Switzerland*

Citation: Grishchenko, M., H. H. T. Prins, R. C. Ydenberg, M. E. Schaepman, W. F. de Boer, and H. J. de Knegt. 2019. Land use change and the migration geography of Greater White-fronted geese in European Russia. Ecosphere 10(8): e02754. 10.1002/ecs2.2754

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 successional 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.

Received 9 August 2018; revised 24 March 2019; accepted 1 April 2019. Corresponding Editor: Paige S. Warren.

† **E-mail:** mikhail.grishchenko@gmail.com

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, Kölzsch 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

1997, Madsen et al. 1999, Hornman et al. 2012). 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 M km^2. 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 km^2, 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. 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, km^2
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	3386	45	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.

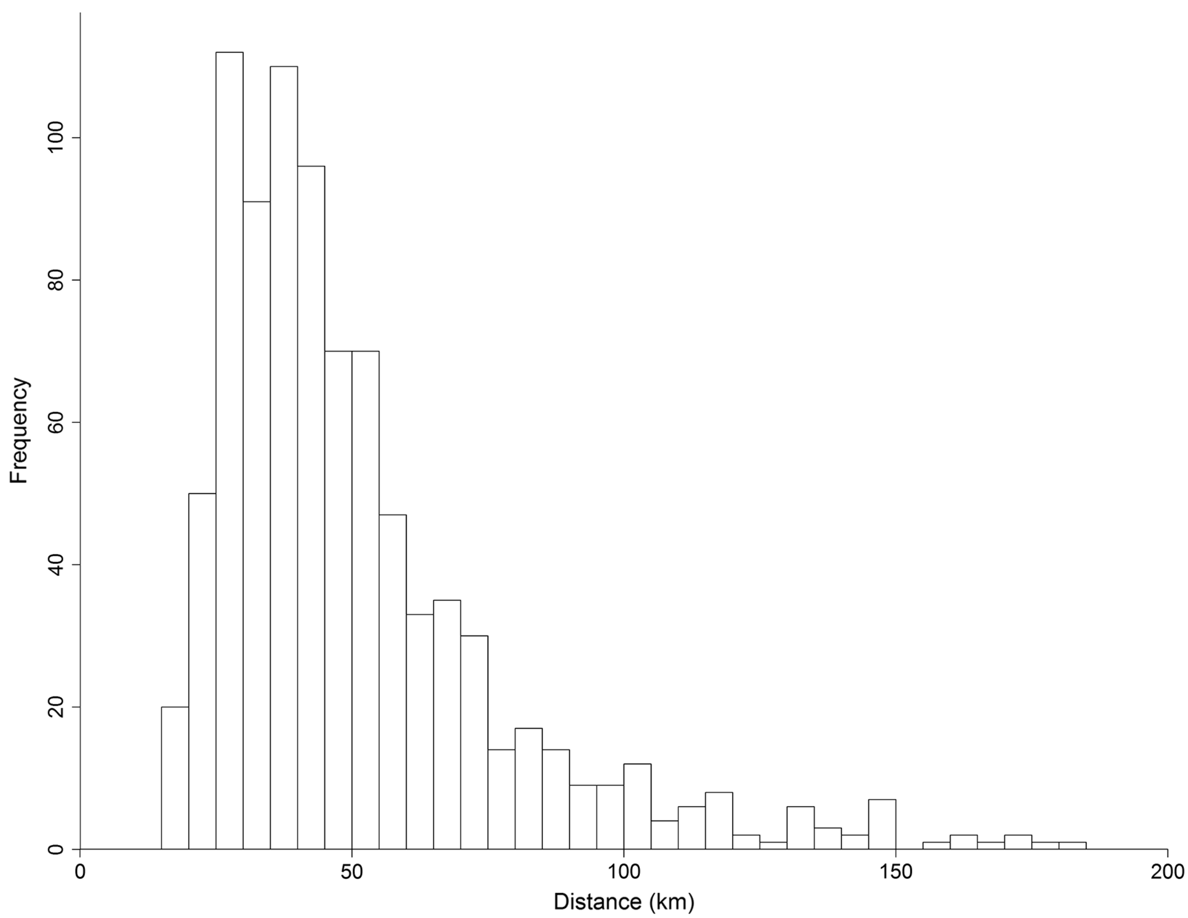

Fig. 1. Distance between nearest-neighbor stopover sites of Atlantic Greater white-fronted Geese in European Russia 1990–2013, based on recoveries of metal rings from shot birds, and sightings of birds with neck collars.

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.

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 Knegt, *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.

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).

Results

The KDE analysis yielded a total of 300 putative stopover sites in European Russia (Fig. 2). In each of the three periods, each stopover was assigned to one of the Voronoi tessellation polygons, which resulted in 200 polygons for period 1, 158 polygons for period 2, and 295 polygons for period 3 (Fig. 3). Despite the increased numbers of metal- and neck-ring recoveries in successive periods (Table 2), the number of stopover sites located by our analysis remained between 200 and 300.

Statistics for the regression analysis are summarized in Table 3. The overall regression was significant (Table 3; $F_{6,\ 646} = 24.99$, $P < 0.001$, adjusted $r^2 = 0.18$). The squared latitude term was highly significant, with the negative coefficient indicating that relative density of stopover sites was highest at mid-latitudes, a pattern that could not be attributed to the co-variates. Distance to the nearest settlement did not have a significant effect, and the effect of distance to the

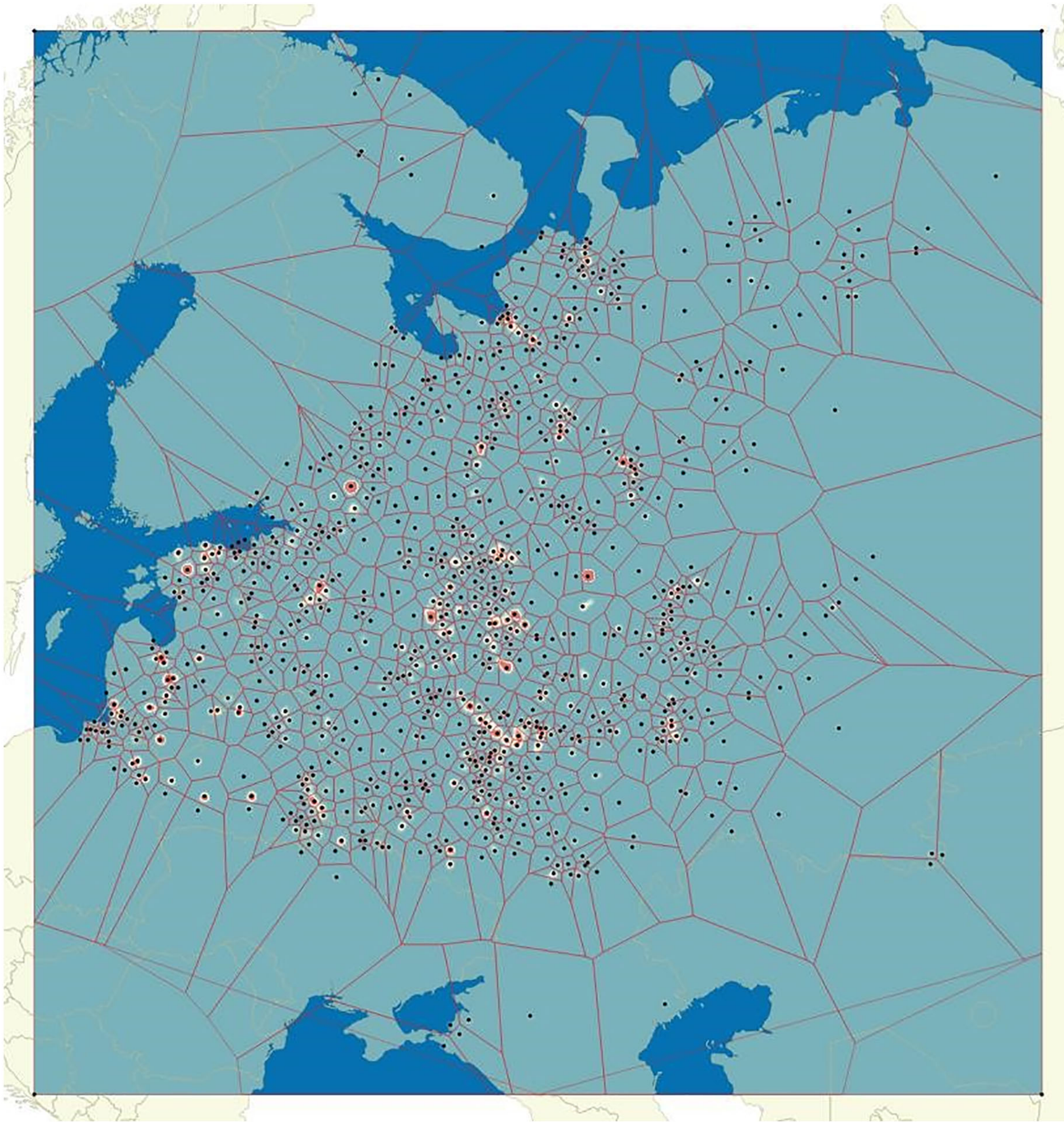

Fig. 2. Stopover site partitioning for period 1 (1960–1990) overlaid with a kernel density estimator of stopover sites. Large polygons (explained in the *Methods* section) were clipped within the study area extent to account for boundary effects.

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.

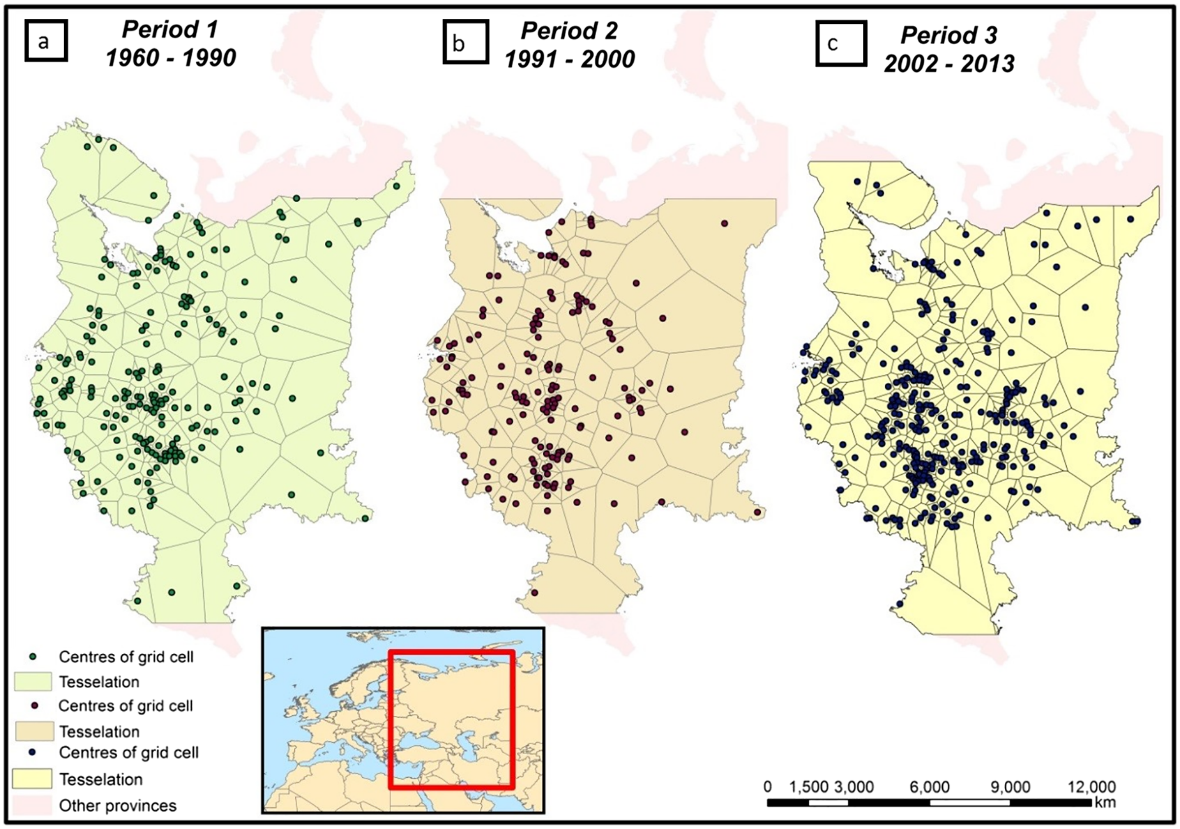

Fig. 3. Space tessellation of the study area in European Russia during three observational periods (period 1, 1960–1990; period 2, 1991–2000; and period 3, 2001–2013).

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.

Table 3. Multiple regression analysis ($F_{6,\ 646} = 24.99$, $P < 0.001$, 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
ln distance to settlement	−0.0644	0.0699	N.S.
ln 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.

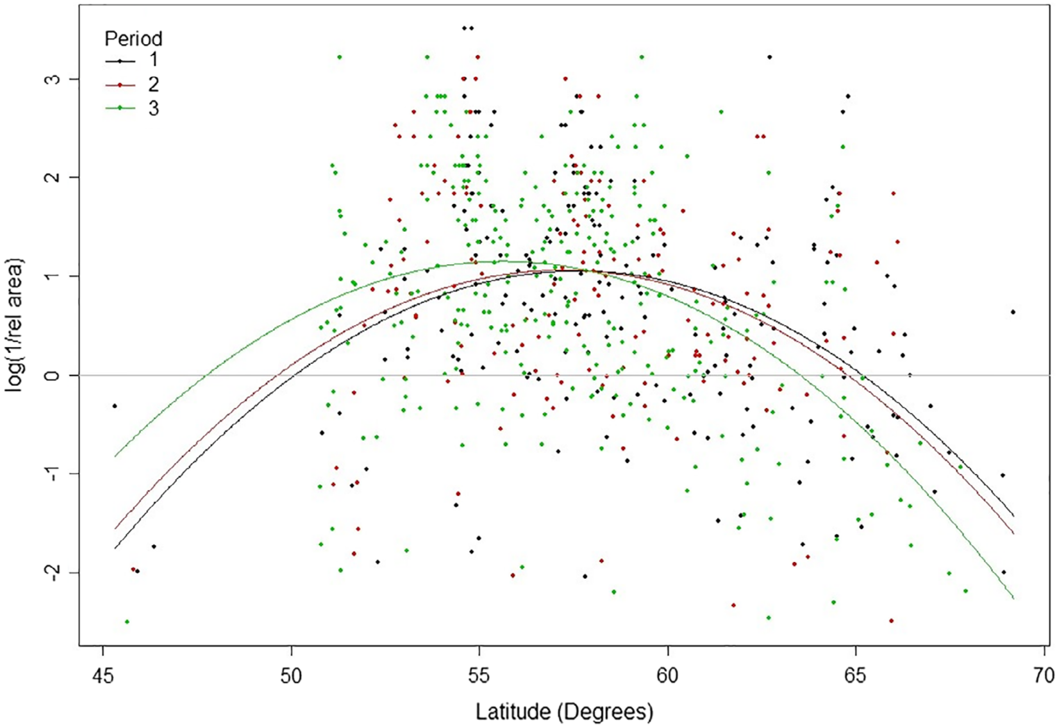

Fig. 4. Log relative density (inverse of relative area) of observed (points) and predicted (lines) stopover sites as function of latitude during three observational periods (period 1: black, 1960–1990; period 2: red, 1991–2000; and period 3: green, 2001–2013). Relative densities increase over time at lower latitudes, yet decrease over time at higher latitudes, thus indicating a southward shift of stopover sites. The southward shift is about 5°.

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 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 geese 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.

Acknowledgments

We acknowledge B. S. Ebbinge and Y. van Randen for providing data on metal ring recoveries and color band sightings of Greater White-fronted geese in Russia. We acknowledge the efforts of the many hunters and birdwatchers, who collected and reported these data. We also thank A. Kölzsch, B. Nolet, and H. Kruckenberg who provided us with satellite tracking data of Greater White-fronted geese. The contribution of M. E. Schaepman is supported by the University of Zurich Research Priority Program on "Global Change and Biodiversity" (URPP GCB). This research was supported by Faunafonds, The Netherlands.

Literature Cited

Arzel, C., J. Elmberg, and M. Guillemain. 2006. Ecology of spring-migrating *Anatidae*: a review. Journal of Ornithology 147:167–184.

Bauer, S., P. Gienapp, and J. Madsen. 2008. The relevance of environmental conditions for departure decision changes en route in migrating geese. Ecology 89:1953–1960.

Braden, K. 2014. Illegal recreational hunting in Russia: the role of social norms and elite violators. Eurasian Geography and Economics 55:457–490.

Cooke, F., C. S. Findlay, R. F. Rockwell, and K. F. Abraham. 1983. Life history studies of the Lesser Snow Goose (*Anser caerulescens caerulescens*). Behavioral Ecology and Sociobiology 12:153–159.

Drent, R. H., A. D. Fox, and J. Stahl. 2006. Travelling to breed. Journal of Ornithology 147:122–134.

Drent, R. H., and H. H. T. Prins. 1987. The herbivore as prisoner of its food supply. Pages 131–147 *in* J. Van Andel, J. P. Bakker, and R. W. Snaydon, editors. Disturbance in grasslands. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Drent, R. H., and R. van der Wal. 1998. Cyclic grazing and the manipulation of the food resources. Pages 271–299 *in* H. Olff, V. K. Brown and R. H. Drent, editors. Herbivores between plants and predators. Blackwell Science, Oxford, UK.

Du, Q., V. Faber, and M. Gunzburger. 1999. Centroidal Voronoi tessellations: applications and algorithms. SIAM Review 41:637–676.

Ebbinge, B. S. 1985. Factors determining the population size of arctic-breeding geese wintering in Western Europe. Ardea 73:121–128.

Ebbinge, B. S., J. Blew, P. Clausen, K. Günther, C. Hall, C. Holt, K. Koffijberg, S. Le Dréan-Quénec'hdu, R. Mahéo, and S. Pihl. 2013. Population development and breeding success of Dark-bellied Brent Geese *Branta b. bernicla* from 1991–2011. Wildfowl 3:74–89.

Eichhorn, G., R. H. Drent, J. Stahl, A. Leito, and T. Alerstam. 2009. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. Journal of Animal Ecology 78:63–72.

Ely, C. R., and D. G. Raveling. 2011. Seasonal variation in nutritional characteristics of the diet of greater white-fronted geese. Journal of Wildlife Management 75:78–91.

Emelchenko, N. N. 2009. A review of white-fronted goose (*Anser albifrons*) migrations in western Palearctic. Zoologicheskiĭ Zhurnal 88:1090–1108.

ESRI. 2016. ArcGIS desktop, release 10.5.1. Environmental Systems Research Institute, Redlands, California, USA.

Farago, S. 2010. Numbers and distributions of geese in Hungary 1984–2009. Ornis Svecica 20:144–154.

Fox, A. D., B. S. Ebbinge, C. Mitchell, T. Heinicke, T. Aarvak, K. Colhoun, and H. Kruckenberg. 2010. Current estimates of goose population sizes in Western Europe, a gap analysis and an assessment of trends. Ornis Svecica 20:115–127.

Fox, A. D., and J. Madsen. 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. Journal of Applied Ecology 34:1–13.

Grishchenko, M., and H. H. T. Prins. 2016. Abandoned field succession in Russia and its potential effect on Corncrake *Crex crex* habitats. Vogelwelt 136:175–184.

Hedenström, A., and T. Alerstam. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Heuermann, N., F. van Langevelde, S. E. van Wieren, and H. H. T. Prins. 2011. Increased searching and handling effort in tall swards lead to a type IV functional response in small grazing herbivores. Oecologia 166:659–669.

Hornman, M., M. van Roomen, F. Hustings, K. Koffijberg, E. Van Winden, and L. Soldaat. 2012. Population trends in wintering and migrating waterbirds in The Netherlands in 1975–2010. Limosa 85:97–116.

Ioffe, G., and T. Nefedova. 2004. From spatial continuity to fragmentation: the case of Russian farming. Annals of the Association of American Geographers 94:913–943.

Jankowiak, Ł., P. Skórka, Ł. Ławicki, P. Wylegała, M. Polakowski, A. Wuczyński, and P. Tryjanowski. 2015. Patterns of occurrence and abundance of roosting geese: the role of spatial scale for site selection and consequences for conservation. Ecological Research 30:833–842.

Jefferies, R. L., and R. F. Rockwell. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. Applied Vegetation Science 1:7–16.

Jonker, R. M., G. Eichhorn, F. Van Langevelde, and S. Bauer. 2010. Predation danger can explain changes in timing of migration: the case of the barnacle goose. PLoS ONE 5:e11369.

Klaassen, M., S. Bauer, J. Madsen, and I. Tombre. 2006. Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. Journal of Applied Ecology 43:92–100.

Koffijberg, K., and E. van Winden. 2014. Naar een populatiemodel voor de Kolgans. Radboud Universiteit Nijmegen, NIOO and Sovon, Nijmegen/Wageningen, The Netherlands.

Kokko, H., H. Pöysä, J. Lindström, and E. Ranta. 1998. Assessing the impact of spring hunting on waterfowl populations. Annales Zoologici Fennici 35:195–204.

Kölzsch, A., G. J. Müskens, H. Kruckenberg, P. Glazov, R. Weinzierl, B. A. Nolet, and M. Wikelski. 2016. Towards a new understanding of migration timing: Slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. Oikos 125:1496–1507.

Kondratyev, A., and H. Kruckenberg. 2013. Barnacle Goose *Branta leucopsis* abundance on Kolguev Island – Current status and history of population growth. Wildfowl 63:56–71.

Kostin, I. O., and J. H. Mooij. 1995. Influence of weather conditions and other factors on the reproductive cycle of red-breasted geese *Branta ruficollis* on the Taymyr Peninsula. Wildfowl 46:45–54.

Kuemmerle, T., J. O. Kaplan, A. V. Prishchepov, I. Rylsky, O. Chaskovskyy, V. S. Tikunov, and D. Muller. 2015. Forest transitions in Eastern Europe and their effects on carbon budgets. Global Change Biology 21:3049–3061.

Lack, D. 1956. Swifts in a tower. Methuen, London, UK.

Madsen, J., G. Cracknell, and T. Fox. 1999. Goose populations of the Western Palearctic. Wetlands International Publication No. 48, National Environmental Research Institute, Aarhus, Denmark.

Mooij, J. H. 1997. The status of White-fronted Goose (*Anser a. albifrons*) in the Western Palearctic. Vogelwarte 39:61–81.

Mooij, J. H., B. S. Ebbinge, I. O. Kostin, J. Burgers, and B. Spaans. 1996. Panmixia in White-fronted geese (*Anser albifrons*) of the Western Palearctic. Pages 107–130 *in* J. H. Mooij, editor. Ecology of geese wintering in the Lower Rhine area (Germany). Dissertation. Wageningen University, Wageningen, The Netherlands.

Nilsson, L., and H. Persson. 2000. Changes in field choice among staging and wintering geese in southwestern Scania, south Sweden. Ornis Svecica 10:161–169.

Polakowski, M., and Z. Kasprzykowski. 2016. Differences in the use of foraging grounds by Greylag Goose *Anser anser* and White-fronted Goose *Anser albifrons* at a spring stopover site. Avian Biology Research 9:265–272.

Polakowski, M., Z. Kasprzykowski, and A. Golawski. 2018. Influence of temperature on the timing of spring arrival and duration of migration in Arctic goose species at a central European stopover site. Ornis Fennica 95:32–40.

Prishchepov, A. V., D. Müller, M. Dubinin, M. Baumann, and V. C. Radeloff. 2013. Determinants of agricultural land abandonment in post-Soviet European Russia. Land Use Policy 30:873–884.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosin, Z. M., P. Skórka, P. Wylegała, B. Krąkowski, M. Tobolka, Ł. Myczko, T. H. Sparks, and P. Tryjanowski. 2012. Landscape structure, human disturbance and crop management affect foraging ground selection by migrating geese. Journal of Ornithology 153:747–759.

Schaub, M., R. Pradel, L. Jenni, and J. D. Lebreton. 2001. Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. Ecology 82:852–859.

Si, Y., Q. Xin, W. F. de Boer, P. Gong, R. C. Ydenberg, and H. H. T. Prins. 2015. Do Arctic breeding geese track or overtake a green wave during spring migration? Scientific Reports 5:8749.

Si, Y., et al. 2011. Distribution of Barnacle Geese *Branta leucopsis* in relation to food resources, distance to roosts, and the location of refuges. Ardea 99:217–226.

Sutherland, W. J. 1998. Evidence for flexibility and constraint in migration systems. Journal of Avian Biology 29:441–446.

van Wijk, R. E., A. Kölzsch, H. Kruckenberg, B. S. Ebbinge, G. J. Müskens, and B. A. Nolet. 2012. Individually tracked geese follow peaks of temperature acceleration during spring migration. Oikos 121:655–664.

Wegren, S. K. 1995. Rural migration and agrarian reform in Russia: a research note. Europe–Asia Studies 47:877–888.

Ydenberg, R. C., and H. H. T. Prins. 1981. Spring grazing and the manipulation of food quality by barnacle geese. Journal of Applied Ecology 443–453.

Zhang, Y., Q. Jia, H. H. T. Prins, L. Cao, and W. F. de Boer. 2015. Individual-area relationship best explains goose species density in wetlands. PLoS ONE 10:e0124972.

Zhao, M., P. Cong, M. Barter, A. D. Fox, and L. E. I. Cao. 2012. The changing abundance and distribution of Greater White-fronted Geese *Anser albifrons* in the Yangtze River floodplain: impacts of recent hydrological changes. Bird Conservation International 22:135–143.

Zimin, V. B., A. V. Artemyev, and N. V. Lapschin. 2002. Survey of spring bird migrations and stopovers in the Olonets fields in Karelia. Pages 7–17 *in* G. A. Noskov, editor. Proceedings of Study of Status and Trends of Migratory Bird Populations in Russia. 4th Issue. World & Family, St. Petersburg, Russia.