Over the last two decades thousands of migrating ruffs (*Philomachus pugnax*) have disappeared from the Western Europe migratory staging sites. These migratory ruffs are partly temperate-breeding birds, but many individuals head towards the Eurasian Arctic tundras where 95% of the global population breeds. This regional decline may represent either: (1) local loss of breeding birds in Western Europe, (2) a global decline, (3) shift(s) in distribution, or (4) a combination of these. To put the declines in Western Europe in context, the breeding areas across northern Eurasia have to be considered. We therefore analyzed Arctic monitoring data from the last two decades (Soloviev & Tomkovich 2009) to detect changes in regional breeding densities using Generalized Additive Modeling (GAM) and Generalized Estimations Equations (GEE). We show that the global breeding population of ruffs has made a significant eastwards shift into the Asian part of the breeding range. In the European Arctic, ruffs decreased during the last 18 years; in contrast, in Western Siberia ruffs increased and in Eastern Siberia no significant population changes could be detected. These changes did not reflect differential climatic changes across the Eurasian breeding range. Instead, they corroborate the finding that during northward migration a growing number of ruffs avoid a major staging site in The Netherlands in Western Europe and instead moved to a more easterly migration route leading into Western Siberia. We thus suggest an unprecedented large-scale population shift of ruffs in response to ongoing agricultural intensification at the traditional staging area in The Netherlands.
Introduction

The extent of phenotypic, genetic and demographic changes of species, in response to environmental dynamics not only provides insights into the limits to species persistence, but also illuminates the involved evolutionary mechanisms. Understanding the resilience of populations currently facing fast alterations of their environment (climate change, habitat loss, and pollution) is of major importance for the maintenance of biodiversity on our planet. Changing environment (Hötker 1991; Donald et al. 2001; Newton 2004) especially agricultural intensification (Pärt & Söderström 1999; Smart et al. 2006; Eglington et al. 2008) significantly affected populations of European birds in recent decades. Herbivorous migrants such as geese have generally profited from the same land-use changes (Pettifor et al. 2000; Fox et al. 2005; Jefferies & Drent 2006; Eichhorn et al. 2009), while most of avian species, including worm- and arthropod-eating breeding shorebirds of the European grasslands species are all in substantial decline (Hötker 1991; Piersma et al. 1996).

Until quite recently, ruffs (*Philomachus pugnax*), a species of shorebird with many unique biological features including strong sexual dimorphism, a lek mating system, the existence of three male types, and extravagant and wonderfully variable plumages...
(Darwin 1871, Lank & Piersma 1988, Lank & Dale 2001), counted as one of the most abundant breeding birds in Western Europe. Despite serious declines as breeding birds, not long ago thousands of ruffs still used wet grasslands in Western Europe as migratory staging areas. During northward migration large numbers headed through Western Europe (Wymenga 1999) towards the Eurasian tundras where over 95% of the world population breed (Zöckler 2002, Zwarts et al. 2009). Ruffs mainly winter in West Africa, but there are also wintering populations in East Africa, South Africa and India.

Ruffs appears to be one of the most flexible migrants. The majority of ruffs, migrating through Western Europe, winter in the West African Sahel region (Zwarts et al. 2009). However, in spring the birds from Sahelian Africa migrate on a broad front and cover Europe as a wide fan. Among the most important and well-studied staging sites are those located in The Netherlands, in Belarus (Karlionova et al. 2007) and in the Crimea, Ukraine (Chernichko et al. 1991).

Ongoing declines of ruffs at staging areas in The Netherlands (Chapter 7) and Sweden (Lindström et al. 2009) may reflect declines in overall population size or local disappearance either or not involving a redistribution. To establish the cause of the declines in migrant ruffs in Europe, we assessed the Eurasia-wide changes in breeding densities on the basis of unique data compiled by the International Breeding Conditions Survey on Arctic Birds (Soloviev & Tomkovich 2009). This study therefore answers a recent call from BirdLife International (Sanderson et al. 2006) that in the light of widespread and steady declines in many Afro-Palearctic migrant birds, the relative importance of factors operating on the birds’ wintering grounds, breeding grounds or on migration routes should be assessed.

**Methods**

Data on trends in numbers of Russian breeding ruffs were obtained from the online database of the International Breeding Conditions Survey on Arctic Birds (Soloviev & Tomkovich 2009). This dataset compiles information from an annual average of 62 circumpolar tundra sites for the period from 1990 to 2007; 185 reports with information on the abundance of breeding ruffs from Eurasia were used. Reports qualified estimates of abundance with assignments to either of three categories: rare, common or abundant.

**Data organization**

The dataset was presented as n observations, defined by three qualitative categories of abundance (rare, common and abundant). Proportional odds logistic regression is commonly used to analyze such data. However, currently it does not allow for non-linear modeling. To avoid this restriction, the initial data was used twice and the three qualitative categories of abundance were transformed into two dummy binary response variables Y1 and Y2 (Table 8.1) (Winkelmann & Boes 2009). In the first dataset the binary response variable Y1 was given 0 values for the initial category rare.
and ‘1’ for the rest of observations, which met the condition “more than rare”. In the second dataset Y2 was set to 1 for the abundant category and Y2 = 0 for “less than abundant”.

Although two separate models for the response variables could be applied, we preferred to unify them into the single model. For this the two obtained datasets were merged into one and introduced a two-level identifier \( \alpha \) (\( \alpha = 1 \) for Y1 and \( \alpha = 2 \) for Y2). This way a new dataset was obtained, with binary response variable \( Y \), identifier variable \( \alpha \) and 2n elements, fully describing the initial information. In addition, to model the autocorrelation structure, a variable representing the unique identification number for each initial observation was introduced.

**Table 8.1.** Data transformation for the analysis. Y1 and Y2 are binary response variables and \( \alpha \) is an identifier variable defining source dataset.

<table>
<thead>
<tr>
<th>Abundance Initial variable</th>
<th>Y1 (( \alpha = 1 )) Response variable</th>
<th>Y2 (( \alpha = 2 )) Response variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rare</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Common</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Abundant</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

**Software packages used**

R 2.8 software (R Development Core Team 2008), with packages “mgcv” for Generalized Additive Modeling (Wood 2004, 2008) and “geepack” for General Estimation Equations (Yan 2002; Yan & Fine 2004) was used for all analyses.

**Generalized Additive modeling**

Despite the qualitative nature of the presented observational data, the above described simple transformation allowed the application of thoroughly developed and reliable modeling methods, appropriate for a binary response variable, to model the abundance of breeding ruffs in the Russian Arctic.

Generalized Additive Modeling (GAM) with a binomial distribution and a logistic link function was applied to visualize the longitudinal changes in population trends:

Model 1: \( Y \sim \alpha + s(\text{Year,Longitude}) \),

where \( s() \) is the smoothing function.

Note that although Generalized Additive Mixed Modeling (GAMM) would have taken into account the consequences of data duplication, GAM was preferred as it was more stable (Wood 2008).

Based on predictions from the GAM model results, two parallel (at the linear
predictor scale) surfaces were drawn: one for the probability of ruffs being more than rare \((\alpha = 1)\) and another one for more than common \((\alpha = 2)\). The model results of population trends distinguished three areas with different population trajectories, and thus a new three-level explanatory variable “range” was created and introduced in further analyses. To ascertain the precise longitudinal boundary values, GAM surfaces were cut at each degree longitude and a linear regression of predicted probability of abundance from year was conducted for each slice. Positive and negative slopes indicated positive and negative trends in ruffs abundance, correspondingly. Longitudinal points with zero slopes (i.e. stable abundance) indicated boundaries of ranges with reversed trends. This allowed us to replace the continuous explanatory variable “longitude” with categorical one called “range”. This new explanatory variable was introduced into the next GAM model, also with binomial distribution and logistic link function:

Model 2: \(Y = \alpha + \text{Range} + s(\text{Year})\cdot\text{Range},\)

where \(s()\) is the smoothing function.

This yielded single factor smoothers \((s_i)\) for each range that were plotted and used for further analysis.

GAM results for the European range were compared with monitoring data collected in Finland (see Väisänen 2006).

**General Estimation Equations**

Because of the small sample sizes, the use of linear models was preferred. To define linear trends in population dynamics within the three ranges, the General Estimation Equations method (GEE) with a binomial distribution, a logistic link function and exchangeable correlation structure was applied. GEE is a way to get valid parameters estimation from GLM in presence of potential autocorrelation of data from the same observation (Zuur et al. 2009). The “geeglm” R-package (Yan 2002, Yan & Fine 2004) with “exchangeable” type of correlation structure was used. Variables year, longitude and range were used to model the abundance of nesting ruffs. The variable longitude was nested in range. The initial model had the following structure:

Model 3: \(Y \sim \alpha + \text{Year} + \text{Range} + \text{Year}:\text{Range} + \text{Range}:\text{Longitude} + \text{Year}:\text{Range}:\text{Longitude}\)

For model simplification, backwards selections with ANOVA comparisons were applied.

**Observer effects**

To test whether variation in the experience of observers could have biased estimates of local ruff abundance, a new factor was created with two levels: “new” for reports from each first-year observer and “experienced” for reports from observers with more than one year of experience. The dataset contained 65 reports from “new” observers and
from “experienced” observers. Observer effect was included as an explanatory variable in all models, but being insignificant it was excluded. This indicates that reports from experienced and newly trained observers were equally informative.

**Temperature trends**

For years 1990 till 2008, average deviations in mean temperatures in June were calculated for three regions within the breeding distribution of ruffs, following the method described by Soloviev et al. (2007). The three regions comprised Finland and the two westernmost ranges from the previous analysis – the European part of the Russian Arctic with Yamal peninsula, and the Western Siberian range. The initiate model had the following design:

Model 4: June_temperature ~ Year*Range

There were no significant temporal autocorrelation patterns and no violation of the homogeneity assumption, so a linear regression model with backwards selection was used (Zuur et al. 2009). Model 4 was repeated to test for average deviations of mean July temperatures.

**Results**

Between 1990 and 2007, no overall global population decline could be detected (Fig. 8.2). Instead, trends in the abundance of breeding ruffs varied with longitude, as indicated by a statistically significant nonlinear interaction between year and longitude in the GAM model of abundance trends (Model 1, p = 0.0005). After grouping sites with similar trends, three longitudinal ranges were distinguished (Fig. 8.2A). The boundaries for the ranges were defined at values of longitude where linear trends of abundance reversed (see Methods, Fig. 8.2C) and represented existing geographical barriers (Fig. 8.2B). In the westernmost part of the range, ruffs decreased; this area comprised the Russian European Arctic plus Yamal Peninsula with a western boundary at 27° and a natural boundary along the Ob River at 73° (hereafter Russian European Arctic). In the central range (from 73° to 97°) the ruff population increased; this area contained Western Siberia and Western Taimyr, and was comprised mostly by lowland areas (hereafter Western Siberia). In the easternmost range, which extended from Central Taimyr (97°) eastwards throughout mountainous Eastern Siberia, ruffs decreased over the last two decades, but only slightly so.

The trends within the detected European and Western Siberian ranges were confirmed by a second model, fitted with General Estimation Equations methods (Model 3). In Eastern Siberia, significant longitudinal variation in trends was found (p = 0.0024). However, due to insufficient sampling in this part of the range, East Siberia had to be excluded from further analyses. Without the sparse data from East Siberia, the effect of variable “longitude” became insignificant and was excluded by backward selection.
Figure 8.2. The abundance of arctic breeding ruffs between 1990-2007, in relation to longitude, as estimated by Generalized Additive Modeling (GAM).

(A) Modeled probability for ruffs to be more than rare. Increase in shading intensity represents a decrease in abundance. Dots are initial data points (small dot – “rare”, medium – “common”, large – “abundant”). Solid lines are the isolines of the GAM model, with numbers indicating probabilities. Dashed lines cut the surface into three regions with similar trends.

(B) The geographical regions underlying the three regions with similar trends. The western region concurs with the Russian part of the European Arctic, the middle region concurs with West Siberia, and eastern region concurs with East Siberia and the Far East.

(C) The relationship between longitude and the long-term trends in abundance of ruffs as estimates by linear slopes of the surfaces obtained with Generalized Additive Modeling (GAM, see panel A). Black line: probability of being more than rare, grey line: probability of being more than common. Horizontal line: a stable situation with slope = 0 found for two points – at longitude 73° and 97° east. These points were used to determine the ranges boundaries as indicated by the vertical dashed lines (see Fig. 8.4).
with ANOVA comparisons. GEE analyses for the Russian European Arctic and Western Siberia allowed estimation of the overall linear slopes for changes in abundance. The slope for decrease in probability of high abundance for the Russian European Arctic was approximately -0.021 for breeding ruffs being ‘more than rare’ and -0.029 for them being ‘more than common’. The slopes for the increase in Western Siberia were 0.029 and 0.07, respectively (Fig. 8.3).

To test for the nonlinear component in the overall trends, GAM analysis was repeated with the categorical explanatory variable “range” instead of the continuous “longitude” variable (Model 2). For the Western Siberian range the best smoother was linear, but for the European part a nonlinear significant smoother with two periods of decrease was detected. It actually revealed two periods of decline: one in the 1990s and another in the 2000s (Fig. 8.4).

**Figure 8.3.** Long-term changes in the abundance probabilities of arctic breeding ruffs in the European (solid lines) and Western Siberian (dashed lines) ranges, as obtained by linear modeling (Generalized linear model (GLM) fitted with General Estimation Equations method (GEE)). Black lines: probability of being more than rare. Grey lines: probability of being more than common.

**Figure 8.4.** Range specific, long-term changes in the abundance probabilities of arctic breeding ruffs in the European and Western Siberian ranges, as obtained with Generalized Additive Modeling (GAM). Response parameter: abundance of ruffs. Ranges boundaries were detected with the GAM model that included longitude (see Fig. 8.2C). Year: 1990-2007.
The analysis of temperature trends revealed no statistically significant terms (F1, 57 = 2.43, p = 0.13 for temperature trend in June; F2, 57 = 0.95, p = 0.91 for temperature trend in July; F1, 57 = 3.17, p = 0.081 for Range effect in June, F2, 57 = 1.77, p = 0.18 for Range effect in July) or interactions (F2, 57 = 1.56, p = 0.22 for June temperature:Year; F2, 57 = 0.95, p = 0.91 for July temperature:Year; Fig. 8.5). Thus no statistically significant changes of June and July temperatures for the last 20 years and no differences in trends between the three analyzed regions were detected.

**Discussion**

Adding on to the previously reported decreases in the temperate breeding ruffs in Western Europe by Zöckler (2002), we demonstrated substantial decreases in the adjacent parts of the European breeding range, the Russian Arctic (Fig 8.6D). Our results were based on qualitative data, but are perfectly consistent with quantitative survey data of ruffs breeding in northern Finland (Fig. 8.6C; Spearman r = 0.73, nyears = 18, p <0.001) (Väisänen 2006). Meanwhile, the declines in Europe were mirrored by an increase in Western Siberia. Here we discuss three possible hypotheses for the observed decline in the European Arctic.

First, changes at the breeding grounds could have lead to a decrease in reproductive success, resulting in lower recruitment into the European Arctic breeding ruffs. However, the proportion of juveniles observed at staging sites during southward migration in autumn has been stable (on average 53.1%, n = 538 following Zwarts et al. 2009). This suggests that reduced breeding success in European Arctic is unlikely to be the reason for the decline in Europe.
Second, deteriorating conditions on the wintering grounds could have carry-over effects on the breeding grounds. Ruffs from Europe migrate to Sahelian Africa (Fig. 1, Zwarts et al. 2009). Thus, the steep decrease in breeding numbers of European ruffs could be explained by hunting or deteriorating habitat conditions in Sahel. Approximate data on annual harvests of ruffs in Mali (Zwarts et al. 2009) do not allow for precise recalculation of population loss. Count data for the Sahel region also lack accuracy, as ruffs are difficult to monitor on the inaccessible floodplains that they prefer (Zwarts et al. 2009). Nevertheless, the count data show no declines in wintering numbers since the early 1990s. Rainfall trends in West Africa were positive rather than negative during this period, and in the most recent years the available amount of suitable habitat may even have increased (Zwarts et al. 2009). Hence we cannot explain the declines in the West European staging area and the European breeding range with population loss at wintering grounds only. Moreover, the increasing West Siberian ruffs partly winter in Sahelian region as well (Zwarts et al. 2009).

Our last hypothesis considers changes along the flyway and suggests a shift of migrating ruffs between migration routes (Chapter 7). According to spring counts, the disappearance of ruffs staging in The Netherlands during northward migration

![Figure 8.6. Summary of population trends of arctic breeding ruffs, and population trends along the Western and Eastern European migration routes. Panel A: the migratory population of The Netherlands (Chapter 7). Panel B: the migratory population of Belarus (Chapter 7). Panel C: the breeding population of Finland (Väisänen 2006). Panel D: the breeding populations of the European part of the Russian Arctic (this study). Panel E: the breeding population in Western Siberia (this study).]
(Fig. 8.6A) coincides with an increase in staging numbers in Belarus (Fig. 8.6B). The timing of migration changed in concordance: ruffs mainly disappeared from the Dutch staging area in the second half of April, and during this same period of time the number of ruffs in Belarus increased. The migration route through Belarus mostly ends at the breeding grounds in Western Siberia or even further east (Zwarts et al. 2009), and our analysis revealed a statistically significant and rapid increase in the abundance of ruffs breeding in Western Siberia (Fig. 8.6E). We thus propose that this increase represents an influx of birds breeding previously in northern Europe. The hypothesis is supported by resighting data: individual birds marked in The Netherlands were indeed resighted on more eastwards migration routes between 2005 and 2008 (Chapter 7).

There are too few data points to precisely determine the timing of the increase in Western Siberia, but it is remarkable that large decreases in the Dutch passage population (Fig. 8.6A) and the European breeding grounds (Fig. 8.6D) coincide with increases in birds staging in Belarus (Fig. 8.6B) and an increase of birds breeding in Western Siberia (Fig. 8.6E). We propose that ruffs have shifted their migration routes eastward as they now seem to largely avoid The Netherlands and may instead prefer migration routes via Eastern Europe which terminate in Western Siberia rather than the European Arctic. What could have caused this spectacular shift? A further comprehensive analysis is needed to define the reasons underlying this process. Here we discuss some of them: divergence in temperature trends and anthropogenic pressure between different parts of the species breeding area and habitat deterioration at its western European staging sites.

Global spring (June) and summer (July) temperature dynamics for the last 19 years did not differ between Finland, European and Western Siberian Russian parts of ruff breeding range (Fig. 8.5). Thus we cannot conclude that the opposing trends in ruff abundance in Europe and Western Siberia were a consequence of local temperature differences. We consider anthropogenic habitat loss at the breeding sites also to be an unlikely explanation for these trends as the European part of Russia is economically closer to Western Siberia than to Finland; the key industry in the North of Russia is oil and gas production, while in Finland economics relies mostly on timber harvesting and agriculture. Thus, we cannot suggest any anthropogenic factors which would identically affect the European part of Russia and Finland, whilst having an opposite effect on Western Siberia.

Land use changes, especially the decrease of water tables and subsequent intensification of agricultural land, have unanimously been regarded as a cause for the declines of temperate breeding ruffs in Western Europe (Delany et al. 2009; Thorup 2006; Zöckler 2002). The migratory ruffs in The Netherlands show the same preferences for wet habitats (Verkuil & de Goeij 2003), and thus land use change is expected to negatively affect staging ruffs. We detected a significant decrease in local staging performance (refueling rates, moult rates) in ruffs migrating through The Netherlands in 2001 – 2008, indicators that were stable in ruffs migrating through Belarus (Chapter 7). The lower performance of ruffs in The Netherlands is correlated with declines of
wet grasslands (which also caused the disappearance of breeding ruffs in temperate Western Europe, Thorup (2006), Delany et al. (2009)), and we thus believe that man-made habitat loss at the staging areas may well explain the eastward shift of northward migrating ruffs.

Regardless the reasons for the redistribution, our analyses show that ruffs are currently living out their potential to quickly react on locally changing conditions by shifting within the range. This finding implies that the population dynamics of avian species with a widespread distribution cannot be evaluated locally, and may need to be considered at a scale even larger than Europe. In ruffs, the response to changing conditions is strikingly fast and seems to occur well within the lifespan of individual birds. This makes us believe that mechanisms, also involving non-genetic inheritance and phenotypic flexibility (Piersma & van Gils 2010), contribute to the resilience of this species to global change.

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We thank Ole Thorup and Åke Lindström for valuable suggestions. We also thank Natalia Karlionova and Pavel Pinchuk for the quantitative data from Belarus. And we deeply appreciate the input of those people who observed ruffs under severe Arctic conditions and were enthusiastic enough to report their data to the Arctic Birds Breeding Conditions Survey of the International Wader Study Group. We thank Rosemary Gibson for improving the English.