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A global population redistribution in a migrant shorebird detected with continent-wide qualitative breeding survey data

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ABSTRACT

Aim Over the last two decades, thousands of northward migrating ruffs (*Philomachus pugnax*) have disappeared from western European staging sites. These migratory ruffs were partly temperate breeding birds, but most 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.

Location Northern Eurasia.

Methods To put the declines in western Europe in context, we analysed Arctic monitoring data from the last two decades (Soloviev & Tomkovich, 2009) to detect changes in regional breeding densities across northern Eurasia. We used a novel approach applying generalized additive modelling (GAM) and generalized estimations equations (GEE).

Results 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. At the same time, in western Siberia, ruffs increased. In eastern Siberia, no significant population changes could be detected. These changes corroborate the finding that during northward migration, growing numbers of ruffs avoided staging areas in the Netherlands and Sweden and started migrating along a more easterly route leading into western Siberia.

Main conclusions We detected an unprecedented large-scale population redistribution of ruffs and suggest that this is a response to loss of habitat quality at the traditional staging site in the Netherlands.

Keywords

Arctic, GAM, GEE, migration, *Philomachus pugnax*, redistribution, ruff, Scolopacidae, waders.

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 evolutionary mechanisms involved (Piersma &

van Gils, 2011). Equally important is the role of such changes for an understanding of the resilience of populations currently facing fast alterations of their environment (climate change, habitat loss and pollution). Changing environments (Hötker, 1991; Donald *et al.*, 2001; Newton, 2004), especially by agricultural intensification (Pärt & Söderström, 1999; Smart

et al., 2006; Eglington *et al.*, 2008), have significantly affected populations of European birds in recent decades. Herbivorous migrants such as geese have been able to profit from these land-use changes (Pettifor *et al.*, 2000; Fox *et al.*, 2005; Jefferies & Drent, 2006; Eichhorn *et al.*, 2009), but most shorebirds of agricultural landscapes are in rapid decline (Hötter, 1991; Piersma *et al.*, 1996).

A unique database compiled by the *International Breeding Conditions Survey on Arctic Birds* (Soloviev & Tomkovich, 2009) provides the opportunity to assess Eurasia-wide changes in breeding densities of these declining shorebirds. Here, we present a novel statistical tool designed to mine this database. The ruff (*Philomachus pugnax*) was used as focal species as it is very common and has wide distribution throughout Eurasia (Fig. 1). Until quite recently, ruffs, a species with many unique biological features including severe sexual dimorphism, an unconventional mating system, the existence of three types of male, and extravagant, and wonderfully variable plumages (Darwin, 1871; Lank & Piersma, 1988; Lank & Dale, 2001; Jukema & Piersma, 2006), was counted as one of the most abundant breeding birds in western Europe (Piersma, 1986). Despite serious declines as breeding birds, not long ago, thousands of ruffs still used wet grasslands in western Europe 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 (Piersma *et al.*, 1996; Zwarts *et al.*, 2009). The majority of ruffs migrating through western Europe overwinter in the West African Sahel region (Zwarts *et al.*, 2009). However, in spring, the birds from Sahelian Africa migrate on a broad front over Europe, but still seem to concentrate on a few important staging areas. Among the best 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 sites in the Netherlands (Verkuil, 2010) and in Sweden (Lindström *et al.*, 2009) may reflect either declines in overall population size or local disappearance, which may or not involve a redistribution. Whatever the nature of the decline, its causes are not agreed upon (Zöckler, 2002; Verkuil, 2010). To provide insight into the nature of the declines in migrant ruffs in Europe, we assessed the Eurasia-wide changes in breeding densities using the *International Breeding Conditions Survey on Arctic Birds* (Soloviev & Tomkovich, 2009). We compare these findings with the changing breeding population in Finland (Väisänen, 2006), counts of migrating ruffs in the Netherlands and Belarus in spring, proportions of young birds in flocks migrating through the Netherlands in autumn and counts of ruffs wintering in West Africa (Zwarts *et al.*, 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-Palaearctic migrant birds, the relative importance of factors operating in the course of the birds' annual cycle should be assessed. This is a step on the way to the integrated research of ruff throughout its annual cycle with the consideration of conditions during each of the life cycles stages (Piersma & Lindström, 2004; Bowlin *et al.*, 2010).

Figure 1 Breeding and wintering areas of the ruff *Philomachus pugnax*. The major migration routes through western and eastern Europe are indicated with lines. In solid dark grey: the western European and Russian Arctic, harbouring c.95% of the global population of the ruff. Light grey: wintering areas (modified after Zwarts *et al.*, 2009). Not indicated: the temperate breeding areas, harbouring minor and strongly declining populations of ruffs. The map is projected in azimuthal equidistance projection (Bivand *et al.*, 2008), centred in the West African major wintering sites. Direct lines from the West Africa are the shortest paths (orthodromes) on the earth surface (Gudmundsson & Alerstam, 1998).

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 data set 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 data set was presented as n observations, defined by three qualitative categories of abundance (*rare*, *common* and *abundant*). Such data are commonly analysed with proportional odds logistic regression; however, current computation tools (Zuur *et al.*, 2007) do not allow for nonlinear modelling. To

circumvent this restriction, the three qualitative categories of abundance were transformed to two dummy binary response variables $Y1$ and $Y2$ (Table 1) (Winkelmann & Boes, 2009). In the first transformation, 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 transformation, $Y2$ 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 a single one in which the two transformations were merged and a two-level identifier α ($\alpha = 1$ for $Y1$ and $\alpha = 2$ for $Y2$) was introduced. With a binary response variable Y , an identifier variable α and $2n$ elements, the initial information was fully described. To model the autocorrelation structure, a variable representing the unique identification number for each initial observation was introduced.

Software packages used

R 2.8 software (R Development Core Team, 2008), with packages 'mgcv' for generalized additive modelling (GAM) (Wood, 2004, 2008) and 'geepack' for generalized estimation equations (Yan, 2002; Yan & Fine, 2004), was used for all analyses.

Generalized additive modelling

Despite the qualitative nature of the presented observational data, the above-described simple transformations allowed the application of generalized additive modelling (GAM) with a binomial distribution and a logistic link function to visualize the longitudinal changes in population trends:

$$\text{Model1} : Y = \alpha + f(\text{Year}_i \times \text{Longitude}_j),$$

where $f()$ is an automatically fitted tensor product smooth.

Note that although generalized additive mixed modelling (GAMM) would have taken into account the consequences of data duplication, we applied GAM as a more stable technique (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

Table 1 Data transformation for the analysis. $Y1$ and $Y2$ are binary response variables, and α is an identifier variable defining source data set.

Initial variable	Response variable	
	$Y1$ ($\alpha = 1$)	$Y2$ ($\alpha = 2$)
Abundance		
Rare	0	0
Common	1	0
Abundant	1	1

results of population trends distinguished three areas with different population trajectories and thus a new explanatory variable 'range' was created and introduced in further analysis. To ascertain the precise longitudinal boundary values, GAM surfaces were cut at each degree longitude and a linear regression of predicted probability of being abundant in a given abundance category from year was conducted for each slice. Positive and negative slopes indicated positive and negative trends in ruff 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 a subsequent GAM model, also with a binomial distribution and a logistic link function:

$$\text{Model 2} : Y = \alpha + \text{Range}_i + f_i(\text{Year}_j),$$

where $f_i()$ is automatically fitted smoothing functions.

This yielded single factor smoothers (f_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).

Generalized estimation equations

To define linear trends in population dynamics within the three geographical areas, the generalized estimation equations method (GEE) with a binomial distribution, a logistic link function and exchangeable association structure was applied. GEE is a way to get valid parameters estimation from generalized linear model (GLM) in the presence of potential autocorrelation of data from the same observation (Zuur *et al.*, 2009). In our case, we had to use this technique as the data set was doubled during the transformation. The function `geeglm` from the 'geepack' R-package (Yan, 2002; Yan & Fine, 2004) with an 'exchangeable' association structure was used. As we had only two observations for each point, we used the most simple form of within-subject correlation – 'exchangeable', that assumes the same correlation coefficient for all observations. 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:

$$\text{Model3} : Y = \alpha + \text{Year} + \text{Range} + \text{Year} \times \text{Range} + \text{Range} \times \text{Longitude} + \text{Year} \times \text{Range} \times \text{Longitude}.$$

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

Observer effects

To test whether variation in the experience of observers could have biased the 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 1 year of experience. The data set contained 65 reports from 'new' observers and 120 from 'experienced' observers. Observer effect was included as an explanatory variable in all models, but being insignificant on all occasions, it was excluded by the process of backward selection. This indicates that reports from experienced and newly trained observers were equally informative.

RESULTS

Between 1990 and 2007, no overall global population decline could be detected (Fig. 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 longitudinally separated geographical areas were distinguished (Fig. 2a). The boundaries for the areas were defined at values of longitude where linear trends of abundance reversed [see Methods, Fig. 2(c)]. In the westernmost part of the range, ruffs decreased in an area covering the Russian European Arctic plus Yamal Peninsula with a western boundary at 27° and a natural boundary along the Ob River at 73° E (Fig. 2b); this westernmost area will be denoted by the name Russian European Arctic. In the central part of the range, from 73 to 97° E, the ruff population increased. This area, called western Siberia, comprised western Siberia and western Taimyr and mainly contained lowland areas. The easternmost part of the range where ruffs decreased slightly over the last two decades was called eastern Siberia that extended from central Taimyr (97° E) throughout the eastern mountains of Siberia (Fig. 2b).

The trends detected within European and western Siberian parts of the range were confirmed by general estimation equations models (Model 3). In eastern Siberia, significant longitudinal variation in the trend was found ($P = 0.0024$), but owing to insufficient sampling in this part of the range, eastern Siberia had to be excluded from further analysis. In fact, without the rather sparse data from eastern Siberia, the effect of variable 'longitude' became insignificant and was excluded by backward selection with ANOVA comparisons. GEE analyses for the Russian European Arctic and western Siberia allowed the estimation of the overall linear slopes for changes in abundance. The linear approximation of the decrease in probability of high abundance for the Russian European Arctic was $c. -0.021$ for breeding ruffs being 'more than rare' and -0.029 for them being 'more than common'. The linear increases for western Siberia were 0.029 and 0.07 , respectively (Fig. 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 part of the range, the best smoother was linear, but for the Russian 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. 4).

Figure 2 The abundance of arctic breeding ruffs between 1990 and 2007, in relation to longitude, as estimated by GAM. Panel (a): Modelled 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 isolines of the GAM model, with numbers indicating probabilities. Dashed lines cut the surface into three geographical areas with similar trends. Panel (b): The geographical areas underlying the three regions with similar trends. The western area concurs with the Russian part of the European Arctic, the middle region (from Ob River to central Taimyr) concurs with West Siberia and eastern area concurs with East Siberia and the Far East. Panel (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 modelling (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° E. These points were used to determine the ranges boundaries as indicated by the vertical dashed lines (see Fig. 4).

Figure 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 modelling [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 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 modelling (GAM). Response parameter: abundance of ruffs. Range boundaries were detected with the GAM model that included longitude (see Fig. 2c). Year: 1990–2007.

DISCUSSION

Modelling species abundance with qualitative data

Our novel methodological approach to analyse qualitative data resulted in the estimates of changing abundance that are consistent with quantitative survey data of ruffs breeding in

northern Finland (Fig. 5(c), Väisänen, 2006). This is an encouragement to do further analyses with the data accumulated in the Arctic Birds Breeding Conditions Survey and indeed other data sets based on qualitative measurements of animal abundance.

Decrease in the western European ruffs

We here demonstrate substantial decreases in the adjacent parts of the European breeding range, the Russian European Arctic (Fig. 5d). As our results for the westernmost part of the range correlated with breeding densities in Finland, we can conclude that the component of the global population of ruffs that breed in European Arctic and migrates through western Europe is decreasing.

Densities of closed migratory populations may be affected by (1) recruitment or (2) survival at breeding, staging or wintering grounds (e.g. Sherry & Holmes, 1995). We must also consider emigration from the western European part of the range, based on the fact that ruffs are genetically monotypic and the interchange of individuals between migration routes (Verkuil, 2010). We now consider each of these possible population bottlenecks in turn.

As the proportion of juveniles observed at staging sites in the Netherlands during southward migration in autumn (Zwarts *et al.*, 2009) has been stable and relatively high (on average 53.1%, $n = 538$), reduced breeding success seems an unlikely reason for the decline of breeding ruffs in the Russian European Arctic and Finland. Low winter survival is another possible reason for the decline. Ruffs from western Europe and the European Russian Arctic winter in Sahelian Africa (Fig. 1; Zwarts *et al.*, 2009) and the steep decline of number of the European breeding birds might be explained by hunting pressure and/or deteriorating habitat conditions in the 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 (Zwarts *et al.*, 2009). 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, it is unlikely that the declines in numbers of ruffs using western European staging sites and the European parts of the breeding range are only because of increased population losses at the Sahelian wintering grounds. Moreover, in the Sahel, European breeding ruffs overlap with western Siberian ruffs (Zwarts *et al.*, 2009), a population that is on the increase.

Survival during the breeding season and recruitment estimates are not available for ruffs. We could assume that conditions for survival in the western Arctic have decreased and/or have improved in the eastern part of the range. There is, however, no detailed information on Arctic conditions to test these assumptions. In general, Arctic habitats are fairly pristine

Figure 5 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 (Verkuil, 2010). Panel (b): the migratory population of Belarus (Verkuil, 2010). 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). Spearman coefficients of correlation between different parts of the ruff areal, their significance and sample sizes are shown in arrow boxes.

and improved growth condition because of global warming are believed to favour ruffs (Zöckler & Lysenko, 2003) because they are found at moderately high densities in forest tundra, unlike many other Arctic breeding shorebirds (Zöckler, 2002). Hence, we cannot confirm that a reduced survival might have contributed to the reduction in the western range. Nevertheless, in-transit survival might indeed have changed in the western part of the range because of the decreased staging performance at the major staging site. We do know that conditions on the major staging site in western Europe have deteriorated. Verkuil (2010) demonstrated that from 2001 to 2008, during spring migration in the Netherlands, body mass gain rates declined and ornament development became less extensive. During these years, body mass gain rates remained constant in the major staging site in eastern Europe, in Belarus. In the Netherlands, which harbours most staging ruffs during northward migration in Europe, over the same period, numbers strongly declined (Verkuil, 2010).

Redistribution of ruff between Europe and western Siberia

Another result of our analysis is the increase in ruff abundance in western Siberia. The fact that decline in abundance of the European breeding birds (Fig. 5d) coincided with an increase in the abundance of ruffs breeding in western Siberia (Fig. 5e) and that the decline of numbers migrating through the Netherlands

(Fig. 5a) coincided with increases in numbers of birds staging in Belarus (Fig. 5b), suggests that these trends are not independent. To see whether the loss of habitat quality in the Dutch staging area (Verkuil, 2010) provoked a decrease in local survival and/or emigration, we considered two possibilities. (1) The increase in numbers of ruffs migrating through Belarus towards western Siberia resulted from reduced competition with western European breeders on the shared wintering grounds in West Africa (because the latter died during migration). (2) Individual birds that previously staged in the Netherlands to breed in northern Europe have started to migrate along an eastern migration route and now end up at a more eastern breeding destination. For (1), we have to assume that the ruffs in European and western Siberian represent clearly different population units. This is neither corroborated by the genetic analyses of Verkuil (2010), nor by the ring recovery data summarized by Zwarts *et al.* (2009), that both suggest population homogeneity and interchange of individuals between flyways. Still, density dependence on the wintering grounds might have accelerated the increase in eastern birds after the decrease in western birds, but it cannot explain why western birds started to decline. The 'redistribution hypothesis' (2) is actually corroborated by ring recovery data (Verkuil, 2010) and cannot be rejected.

Regardless of the mechanisms of the redistribution, our analyses suggest that ruffs are currently responding quickly to locally changing conditions, with major shifts occurring well within the life spans of individual birds. This implies that the

population dynamics of widespread birds cannot be evaluated locally or even at a European scale.

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