Effects of flyway-wide weather conditions and breeding habitat on the breeding abundance of migratory boreal waterbirds

Diego Pavón-Jordán, Andrea Santangeli and Aleksi Lehikoinen

1 The Helsinki Lab of Ornithology (HelLO), Finnish Museum of Natural History, FI-00014 University of Helsinki, Finland

*Corresponding author: diego.pavon-jordan@helsinki.fi, Tel. +3584445061210

Aleksi Lehikoinen: aleksi.lehikoinen@helsinki.fi

Andrea Santangeli: andrea.santangeli@helsinki.fi

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ABSTRACT

Anthropogenic habitat loss and climate change are among the major threats to biodiversity. Bioclimatic zones such as the boreal and arctic regions are undergoing rapid environmental change, which will likely trigger changes in wildlife communities. Disentangling the effects of different drivers of environmental change on species is fundamental to better understand population dynamics under changing conditions. Therefore, in this study we investigate the synergistic effect of winter and summer weather conditions and habitat type on the abundance of 17 migratory boreal waterbird species breeding in Finland using three decades (1986–2015) of count data. We found that above-average temperatures and precipitations across the western and northern range of the wintering grounds have a positive impact on breeding numbers in the following season, particularly for waterbirds breeding in eutrophic wetlands. Conversely, summer temperatures did not seem to affect waterbird abundance. Moreover, waterbird abundance was higher in eutrophic than in oligotrophic wetlands, but long term trends indicated that populations are decreasing faster in eutrophic than in oligotrophic wetlands. Our results suggest that global warming may apparently benefit waterbirds, e.g. by increased winter survival due to more favourable winter weather conditions. However, the observed population declines, particularly in eutrophic wetlands, may also indicate that the quality of breeding habitat is rapidly deteriorating through increased eutrophication in Finland which override the climatic effects. The findings of this study highlight the importance of embracing a holistic approach, from the level of a single catchment up to the whole flyway, in order to effectively address the threats that waterbirds face on their breeding as well as wintering grounds.
INTRODUCTION

Understanding how global environmental change affects abundance and population dynamics of wildlife is a core topic in ecology and conservation biology (e.g. Begon et al. 1994) and has been widely studied in the past century. The rapid and continuous human-induced alteration of the majority of Earth’s ecosystems has been indicated as the most important cause of the global biodiversity loss (e.g. Pimm et al. 2006). However, evidence is accumulating that climate change is becoming a major threat for most taxa (Parmesan 2006, Thomas and Williamson 2012). Even though the future global climate scenarios are bound with uncertainty, changes in climate to date have gone beyond the expected natural variability (IPCC 2013). Furthermore, the climate is not changing at the same speed and direction across the globe, with the arctic and boreal zones undergoing the fastest changes (IPCC 2012, 2013).

Climate change can affect species by directly modifying their physical environment, e.g. through variation in temperature that may trigger toxic algal and cyanobacteria blooms, loss of food and protection resources (i.e. underwater vegetation) and outbreaks of diseases such as botulism (Moss et al. 2011). In addition, climate change can also trigger changes in inter-specific interactions such as competition for resources, host-parasite interactions and predator-prey dynamics (Parmesan 2006). In this context, species that inhabit bioclimatic regions undergoing rapid climate change during, at least, part of their life cycle are thought to be at greatest risk from rapidly changing climatic conditions (Gonzalez et al. 2010) but also from continuous habitat transformation (Stoate et al. 2009). Furthermore, aquatic ecosystems are especially threatened by climate change (Moss et al. 2011, Guareschi et al. 2015), which may accelerate the speed at which wetland dependent species lose their optimal habitat. These species may thus be in urgent need for adaptive conservation actions (e.g. Mawdsley 2011). However developing conservation measures for species threatened by climate change is not a trivial task, particularly for bird species breeding in the arctic and boreal regions, as most of them are migratory, spending different phases of their annual cycle in various bioclimatic
zones of the planet. Migratory species may be more vulnerable to climate change because of the differential speed and severity of changes in climate in different areas where they occur throughout the annual cycle. This may increase the risk of phenological mismatches (Knudsen et al. 2011, Pearce-Higgins and Green 2014).

The majority of waterbird species breeding in the arctic and boreal regions are predicted to suffer the most from climate change during the breeding season but also throughout the entire annual cycle (Guillemain et al. 2013, Fox et al. 2015, Lehikoinen et al. 2016a, b). However, it has been shown that waterbirds are highly responsive to changes in weather conditions as compared to other groups of birds (Brommer 2008). Specifically, waterbirds seem to be able to shift their wintering (Zipkin et al. 2010, Lehikoinen et al. 2013) and breeding (e.g. Østenes and Kroglund 2015) distributions and/or to modify their phenology (Rainio et al. 2006, Hansson et al. 2014) in response to climate change. Given their high ecological, economic and societal value, coupled with their widespread population declines owing to habitat loss and climate change, waterbirds constitute a group of species of high conservation concern (Green and Elmberg 2014, Guareschi et al. 2015). As a result, most waterbird species and their key habitats are nowadays protected under international legislation and agreements, such as the Convention on Migratory Species (CMS), the RAMSAR Convention, African-Eurasian Waterbird Agreement (AEWA) and the Natura2000 network under the EU Birds Directive and the EU Habitats Directive. However, effective evidence-based conservation can only be achieved if fundamental ecological knowledge such as the drivers of change in populations, is available (Courchamp et al. 2015). For waterbirds in particular, a good understanding of the drivers of change across their annual cycle is often lacking. Hence, disentangling the effects of habitat type and quality and climatic conditions on waterbird population dynamics can yield knowledge relevant for designing new or adjust existing conservation measures.

Here we use a long-term dataset to study how different drivers of environmental change affect population dynamics of waterbirds breeding in the boreal region of Europe. In particular, we assess
the effect of weather conditions during the breeding and the wintering season on the combined
abundance of 17 migratory waterbird species breeding in Finland in the past three decades. We also
investigate whether such climatic effects differ between three contrasting breeding habitat types: (1)
oligotrophic wetlands, (2) naturally eutrophic wetlands and (3) human-influenced wetlands
surrounded by agricultural landscapes and urban areas with large nutrient load. We predict that mild
weather conditions during winter increase waterbird numbers recorded during the following breeding
season through improved survival (Guillemain et al. 2013, Gunnarsson et al. 2012). Furthermore,
increasing temperature in summer should improve breeding success (Fox et al. 2015), thereby
contributing to increased breeding numbers with one year lag. However, these impacts of climatic
conditions may be conditional to the type of breeding habitat, which may potentiate or counteract the
climatic effects. Last, we predict that, in general, trends in breeding waterbird numbers will differ by
habitat type, with more negative trends in habitats with higher nutrient load (wetlands in
agricultural/urban areas) than in oligotrophic wetlands due to hyper-eutrophication process (e.g. Moss
et al. 2011), as also previously shown by Lehikoinen et al. (2016b). Our study provides one of the
very few examples where impacts of climatic and other environmental variables, and their
interactions, have been simultaneously considered. We believe that the evidence provided here could
help to guide international conservation measures in the context of climate change adaptation and
hunting regulations, and ultimately ensure the long-term viability of waterbird populations.

METHODS

Waterbird count data

Here we use a long-term (1986–2015) dataset on waterbird breeding abundance in Finland. Overall,
110 077 breeding pairs of 17 migratory species of waterbirds were counted in the 30 years of study
(see Supplementary Material Appendix 1 Table A1 for details). Although all 17 species are regular
breeders in Finland (Valkama et al. 2011), there are substantial differences in abundance (i.e. breeding population) between them and also large inter-annual variation in breeding numbers within species.

The breeding waterbird census in Finland has been coordinated by the Finnish Museum of Natural History since 1986. This census consists of two visits to each surveyed wetland per year. A first visit is carried out in early May and a second visit in late May in order to account for the different timing between early (e.g. mallard, common pochard and common goldeneye) and late (e.g. Eurasian wigeon, tufted duck, red-breasted merganser) breeding species. Hence, for this study, we used only count data derived from the first visit for the early breeding species, and only from the second visit for the late breeding species within each year. Each census is carried out by experienced volunteer bird watchers which are assigned a route or several wetlands to be surveyed (the detailed census method is described in Koskimies and Väisänen [1991]).

Habitat data

The census sites include wetlands of varying sizes and with different levels of nutrient load. All wetlands are originally classified into eight habitat categories (see Lehikoinen et al. 2016b for a complete description of the eight categories), but for the purpose of this study we merged these categories, resulting in three habitat classes: (1) oligotrophic wetlands with no vegetation, (2) naturally eutrophic wetlands surrounded by forests, peatlands or reed beds and (3) eutrophic wetlands surrounded by agricultural land or urban areas where the eutrophication process has been at least partly caused by human actions. The merging was done in order to reduce model complexity and make results more easily interpretable while retaining biologically meaningful habitat categories. Although the habitat classification that we used here refers to the physical characteristics of the wetlands, these could be seen, to some extent, as different levels of habitat quality (Lehikoinen et al. 2016b). In this sense, the habitat quality would be highest in oligotrophic wetlands, intermediate in
naturally eutrophic and lowest quality in wetlands surrounded by farmland and urban areas due to high levels of human pressure and disturbance as well as potentially high levels of eutrophication.

The study sites included in the Finnish breeding waterbird census scheme are distributed across Finland, covering a large latitudinal gradient (Fig. 1). For the purpose of this study, we selected wetlands that were surveyed more than 2 years since the start of the monitoring scheme in 1986 (n = 1280 wetlands). Not all selected sites were monitored every year (range 110–873 monitored sites per year) but the number of censused sites was relatively balanced over the study period (Supplementary Material Appendix 1, Fig. A1). All censuses are carried out well before the reed beds cover the shores to ensure optimal visibility during the census, thereby maximizing detectability. The size (hectares) of each wetland was calculated *a posteriori* using GIS tools.
Weather data

The winter North Atlantic Oscillation Index (hereafter NAOI) was used in this study as a proxy for the general winter weather conditions that the waterbirds considered in this study face across their main wintering areas. The NAOI is calculated as the difference between the normalized sea level pressures in Reykjavik (Iceland) and Lisbon (Portugal) since 1864 (Hurrell et al. 2016). In general, positive values of NAOI are associated with higher temperature and precipitation during winter than average in western and northern Europe. Positive values of NAOI are also associated with above-average rainfall in northern Europe in winter, but also to drier than average winters in southern Europe. The opposite pattern is true for negative values of NAOI (Hurrell et al. 2016). Monthly NAOI data related to Western Europe were downloaded from http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml. In order to obtain a single value for the “general conditions of the winter in western Europe” prior to the breeding season, we averaged the NAOI values of December, January and February each winter.

As a measure of general summer weather conditions, we downloaded June temperature from 1986 to 2013 for the two 5° x 5° grids covering most of Finland (available at the Climate Research Unit of the University of East Anglia’s website: http://www.cru.uea.ac.uk/). The June temperature values for each year in both grids (see above) were then averaged to obtain a single June temperature value per year. Because we assume that summer weather conditions mainly affect breeding success, we can expect breeding numbers in a given year to be linked to the amount of recruits of young individuals from the previous breeding season, survival of which may be also affected by summer weather conditions during the fledgling period (Koskimies and Lahti 1964, Steen et al. 2014, Arzel et al. 2015). In Finland, the brood-rearing phase of most species occurs during June (e.g. Oja and Pöysä 2007, Arzel et al. 2015). Therefore we decided to model the waterbird counts in year $t$ as a function of summer weather conditions in the preceding year, $t-1$. That is, we related breeding waterbird
abundance in year, e.g. 1991, to weather conditions in summer (mean June temperature) 1990 (see Lehikoinen et al. 2016a).

Interactions

We included three two-way interactions in our model (see below) to assess three different processes that may be important for waterbird population dynamics. It has been shown that population trends of several species of waterbirds breeding in Finland differ depending on the type of habitat they use for breeding (oligotrophic vs. eutrophic; Lehikoinen et al. 2016b). We took this comparison one step further by creating a three-categories habitat variable, differentiating naturally eutrophic wetlands from those under large anthropogenic impacts close to urban and farmland areas. Hence, we defined an interaction to quantify different population trends over time in the three habitat types (‘year’ × ‘habitat type’). Second, we wanted to investigate whether the impact of weather conditions on breeding numbers differed between habitats. Because we considered two weather variables relating to winter and summer weather conditions, we defined two interactions to quantify whether possible effects of these two weather variables on breeding numbers differ according to the habitat type where birds have been found breeding (i.e. ‘winter weather conditions’ × ‘habitat type’ and ‘summer temperature’ × ‘habitat type’).

Statistical analysis

Our main aim was to assess the effects of winter and summer weather conditions, habitat type, and the interaction of weather and habitat on the combined abundance of 17 migratory waterbird species breeding in Finland. Due to the nature of our data, we a priori expected to find large variation in the count data within and between species, as well as a large number of zeroes (i.e. several wetlands per year where a species was not observed, zero inflation). As expected, the dispersion statistic (e.g. Zuur
and Ieno 2016a, b) of the Poisson Generalized Linear Mixed Models (GLMM) fitted to the data showed that the model was overdispersed. Hence, we fitted the next model in complexity, a Negative Binomial GLMM (see Zuur and Ieno 2016a). This provided a good fit after checking for overdispersion, heterogeneity and residual patterns and non-linearity (see Zuur et al. 2009, 2010, Zuur and Ieno 2016a). Thus, there was no need to fit a zero-inflated model. To account for different correlation structures in our data, we defined ‘Year’ as a random term (we have several observations each year and those observation within the same year are likely to be more similar than observations between years). In addition, we defined a random effect of ‘Species’ nested within ‘Site’ (we have multiple observations from the same site and many species per site). Following the recommendations by Zuur and Ieno (2016b), the mathematical notation for the statistical model fitted (crossed and nested GLMM NB) is denoted as follows:

\[
\begin{align*}
\text{Count}_i &\sim NB(\mu_i, K) \\
E(\text{Count}_i) &= \mu_i \quad \text{and} \quad \text{var}(\text{Count}_i) = \mu_i + \mu_i^2 \div K \\
\mu_i &= e^{\eta_i} \\
\eta_{ijrk} &= W_{ijrk} + S_{ijrk} + H_j + Year_{ijrk} + Year_{ijrk}^2 + Count_{ijrk-1} + X_j + Y_j \\
&\quad + W_{ijrk} \times H_j + S_{ijrk} \times H_j + Year_{ijrk} \times H_j + Year_i + Site_j + Species_k \\
&\quad (\text{eqn.1}) \\
Year_i &\sim N(0, \sigma_{year}^2) \\
Site_j &\sim N(0, \sigma_{site}^2) \\
Species_k &\sim N(0, \sigma_{species}^2)
\end{align*}
\]
Where \( \eta_{i,j,k,l} \) is the \( i^{th} \) observation (number of breeding pairs) of species \( k \) in site \( j \) in year \( l \). \( W \) is the NAOI value for winter and \( S \) represents the weather conditions during the preceding summer. Year and Year\(^2\) are continuous variables depicting linear and quadratic trends in counts over the study period, because such trends have been shown by earlier studies (Pöysä et al. 2013, Lehikoinen et al. 2016b). \( H_j \) is the habitat type in site \( j \). Count is the autoregressive (AR) term (log-transformed count of breeding pairs of species \( k \) in site \( j \) the preceding breeding season, \( l-1 \)) to account for potential temporal autocorrelation and density dependence. \( X \) and \( Y \) depict the longitude and latitude of site \( j \) to account for potential spatial patterns.

The main objective of this study was first, to assess the overall effect of weather and habitat variables on the breeding abundance of waterbirds (i.e. main effects) and, second, to assess the joint effect of weather and habitat on the abundance (i.e. interactions). Therefore, our modelling approach consisted in two steps: first, we ran the model in (eqn. 1) without the interactions to assess the overall effects of the covariates that are included in the interactions in the model in (eqn. 1). Second, we ran the model in (eqn. 1) to assess the effect of the interactions. After running the model in (eqn.1), we proceeded with model selection only on the interactions (i.e. only interactions were dropped from the full model if non-significant until all the remaining interactions in the model were significant; Bolker 2008, Bolker et al. 2008, Zuur and Ieno 2016b). We did this in order to be able to interpret correctly the main effects of the covariates when the interactions were non-significant (Burnham and Anderson 2002, Arnold 2010).

All models were fitted using the package \texttt{glmmTMB} (Magnusson et al. 2016) in R 3.2.3 (R Core Team 2015). All continuous covariates were standardized (zero mean, unit standard deviation) in order to make all coefficients comparable and to reduce correlation between linear and quadratic effects of the covariate ‘Year’. Collinearity among the covariates was assessed using the Variance Inflation Factor (VIF) analysis. All VIF values were well below the threshold of three, suggesting low collinearity among them (Zuur et al. 2009). We also inspected spatial correlograms based on the
model residuals (Zuur et al. 2009) in order to detect any sign of spatial autocorrelation (Supplementary Material Appendix 1, figs. A2). We applied a similar procedure using autocorrelation function (ACF) to detect any sign of temporal autocorrelation (Zuur et al. 2010) in the residuals. No signs of spatial or temporal autocorrelation were detected in the residuals of the model.

RESULTS

The model explaining abundance of waterbirds breeding in Finland indicates that, among the weather variables, winter NAO have an overall strong positive effect on waterbird numbers during the following breeding season (mean estimate and SE = 0.035 ± 0.005, Z = 6.77, p < 0.001; statistics derived from a model where only main effects were included; see methods above). Conversely, summer temperatures were found to have no overall effect on breeding waterbird abundance recorded in Finland during the following year (mean estimate and SE = -0.003 ± 0.005, Z = -0.54, p = 0.59; statistics derived from a model where only main effects were included). As expected, we found that abundance of breeding waterbirds in one year is positively related to the abundance in the preceding year, and also positively related to the size of the wetland (i.e. the larger the wetland, the greater the abundance; see Table 1). Across Finland, abundance of breeding waterbirds was highest towards the east of the country (Table 1), and was also higher in the two habitats with high nutrient load as compared to oligotrophic wetlands (mean estimate and SE for ‘naturally eutrophic wetlands’ = 1.039 ± 0.043, Z = 23.85, p < 0.001; and mean estimate and SE for ‘eutrophic wetlands surrounded by agricultural/urban areas = 1.199 ± 0.046, Z = 25.83, p < 0.001; statistics derived from a model where only main effects were included). While breeding waterbird numbers have been generally declining across Finland, this decline was typically non-linear with a particularly severe drop in numbers during the most recent years (mean estimate and SE = -0.039 ± 0.010, Z = -4.08, p < 0.001; statistics derived from a model where only main effects were included).
Interestingly, we found evidence that the impact of winter conditions and the population trends differ according to the main habitat type where the birds are found breeding (see significant interactions in Table 1).

### Table 1. Estimated regression parameters, standard errors, z-values and P-values for the NB GLMM presented in eqn (1) after performing model selection on the non-significant interaction*. ‘Habitat’ is a categorical covariate with three levels (see methods). Here we present the results using the oligotrophic habitat type as a base level and the P-values showed are the corrections for the intercept for the other two habitat types (see e.g. Zuur and Ieno 2016b). The same applies to the interactions.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.740</td>
<td>0.710</td>
<td>-5.270</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Winter weather</td>
<td>-0.002</td>
<td>0.015</td>
<td>-0.140</td>
<td>0.893</td>
</tr>
<tr>
<td>Summer weather</td>
<td>-0.002</td>
<td>0.005</td>
<td>-0.410</td>
<td>0.680</td>
</tr>
<tr>
<td>Year</td>
<td>-0.046</td>
<td>0.024</td>
<td>-1.940</td>
<td>0.053</td>
</tr>
<tr>
<td>Year²</td>
<td>-0.039</td>
<td>0.010</td>
<td>-4.100</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Habitat (naturally eutrophic)</td>
<td>1.016</td>
<td>0.045</td>
<td>22.470</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Habitat (surrounded by agri/urban)</td>
<td>1.173</td>
<td>0.048</td>
<td>24.530</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Wetland Size</td>
<td>0.502</td>
<td>0.020</td>
<td>25.200</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Count preceding year</td>
<td>0.218</td>
<td>0.005</td>
<td>42.210</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Latitude</td>
<td>-1.193</td>
<td>0.645</td>
<td>-1.850</td>
<td>0.064</td>
</tr>
<tr>
<td>Longitude</td>
<td>3.926</td>
<td>1.192</td>
<td>3.290</td>
<td>0.001</td>
</tr>
<tr>
<td>Winter : Habitat (naturally eutrophic)</td>
<td>0.045</td>
<td>0.018</td>
<td>2.600</td>
<td>0.009</td>
</tr>
<tr>
<td>Winter : Habitat (surrounded by agri/urban)</td>
<td>0.038</td>
<td>0.016</td>
<td>2.280</td>
<td>0.023</td>
</tr>
<tr>
<td>Year : Habitat (naturally eutrophic)</td>
<td>-0.022</td>
<td>0.027</td>
<td>-0.840</td>
<td>0.403</td>
</tr>
<tr>
<td>Year : Habitat (surrounded by agri/urban)</td>
<td>-0.065</td>
<td>0.026</td>
<td>-2.510</td>
<td>0.012</td>
</tr>
<tr>
<td>Summer : Habitat (naturally eutrophic)</td>
<td>0.019</td>
<td>0.017</td>
<td>1.120</td>
<td>0.261</td>
</tr>
<tr>
<td>Summer : Habitat (surrounded by agri/urban)</td>
<td>0.031</td>
<td>0.017</td>
<td>1.790</td>
<td>0.073</td>
</tr>
</tbody>
</table>

* Note that we also show the estimated regression parameter, standard error, z-values and P-values for the non-significant interaction between ‘Summer weather’ and ‘Habitat’ (see Zuur and Ieno 2016b), extracted from the full model showed in (eqn. 1) before performing model selection (see methods).

Specifically, effects of winter weather conditions were more positive for the fraction of the waterbird population breeding in naturally eutrophic wetlands and wetlands surrounded by agricultural land and urban areas compared to populations breeding in oligotrophic wetlands (interaction between winter
weather and habitat in Table 1). Moreover long-term population trends were significantly more
negative for the fraction of the population breeding in wetlands surrounded by agricultural land and
urban areas compared to that breeding in oligotrophic and naturally eutrophic wetlands (see the
interaction between year and habitat type in Table 1).

DISCUSSION

Here we provide strong evidence of the impact of winter weather conditions throughout the flyway
on boreal waterbird numbers breeding at high latitudes in Europe. We also show that the impact of
winter weather has a different magnitude according the habitat type which waterbirds use for
breeding. In addition, breeding waterbird numbers recorded in Finland are highest in the south and
east of the country, and in large sized wetlands. Results also indicate that breeding waterbirds have
been generally declining in Finland, with the magnitude of this decline being particularly important
in eutrophic wetlands surrounded by agricultural land and urban areas that currently support the
largest populations of breeding waterbirds. We believe that the observed declines are true population
declines and not caused by shifts in species populations as has been observed during wintering season
(Lehikoinen et al. 2013, Pavon-Jordan et al. 2015). It is unlikely that large number of birds would
have moved to breed outside Finland because breeding ducks are typically site faithful to their
breeding areas (Dow & Fredga 1983, Öst et al. 2012, Saurola et al. 2013, our results positive
autoregressive term). In addition, Finnish breeding bird atlas from the same study period suggest that
11 of our study species have shifted their distribution on average 24 kilometres northwards, which is
a similar rate of shift as in other bird species (Brommer et al. 2011).
The result that breeding waterbird numbers are highest after winters with above-average temperature and rainfall in western and northern Europe and drier than average in southern Europe (conditions depicted by high NAOI values) largely matches our expectations. Moreover, the largest positive effect of winter weather on waterbirds breeding in naturally eutrophic wetlands has also biological sense and conservation implications. Drier winters in southern Europe may potentially reduce the quality and availability of wetland habitats used by many wintering waterbirds (Gordo et al. 2011). However, alongside a possible habitat deterioration in southern Europe (Rendón et al. 2008, Longoni 2010, Márquez-Ferrando et al. 2014), the concomitant wet and mild conditions in western and northern Europe may represent optimal conditions for wintering waterbirds that could largely counterbalance the possible negative impacts of changed climate in southern Europe. Furthermore, the core wintering area of most of our study species winter is located in western Europe and only a smaller proportion of the population wintering in southern Europe (Wetlands International 2012, Fox et al. 2016).

The simultaneous changes in winter towards wet and mild conditions in Northern Europe may play a synergistic role in enhancing winter survival of waterbirds. While above-average precipitation in winter may increase habitat availability (Rendón et al. 2008), above-average temperatures may favour the use of such increased habitat by boreal waterbirds that would have otherwise retreated further south in Europe (Guillemain et al. 2013, Fox et al. 2015). Wetlands in northern Europe were completely frozen up to few decades ago but are now largely ice-free and available for overwintering waterbirds (Lehikoinen et al. 2013, Fox et al. 2015, Pavón-Jordán et al. 2015). Overall, suitable winter conditions in Northern and western Europe may allow waterbirds to shorten their migration distance, reduce energetic costs for thermoregulation and migration, and initiated breeding earlier and in better body condition. The assertion above closely matches our results of a positive impact of mild winter weather conditions (i.e. high NAOI values; above-average temperature and precipitation) on breeding numbers. Other studies reported that reduced migration distances can increase waterbirds’ over-
winter survival due to reduced movement costs and decreased intra- and inter-specific competition for food resources, resulting in better foraging opportunities (Elmberg et al. 2014). Moreover, mild winter weather was also associated with decreased thermoregulatory costs (Guillemain et al. 2013, Dalby et al. 2013, Fox et al. 2015), with improved body condition before spring migration (Guillemain et al. 2010, Fox and Walsh 2012), earlier departure from the wintering sites (Gordo 2007, Knudsen et al. 2011, Donnelly et al. 2015) and potentially earlier arrival to the breeding grounds by waterbirds (Murphy-Klassen et al. 2005, Rainio et al. 2006, Arzel et al. 2014, Chambers et al. 2014).

The stronger positive impact of improved winter weather conditions on birds breeding in eutrophic wetlands is interesting. Waterbird populations in eutrophic wetlands are declining at a steeper pace compared to those in oligotrophic wetlands, suggesting that the quality of eutrophic wetlands in Finland may be rapidly deteriorating (see discussion below). As a result, the positive effect of improved winter weather may become most manifest for those populations breeding in an already poor quality habitat, such as eutrophic wetlands. Conversely, improved winter weather conditions may only represent a marginal benefit, and thus unnoticeable statistically, for waterbird populations breeding in a somewhat stable habitat type in terms of trends in quality, as represented by the oligotrophic wetlands in this study.

*Waterbird abundance and trends by habitat type*

The observed population decline of waterbirds, particularly those breeding in eutrophic wetlands surrounded by farmland and urban areas, sounds alarming for the conservation of this important guild. This is particularly so given that eutrophic wetlands support the highest waterbird numbers in Finland. The declining trend may sound apparently contradictory within the current global warming context; favourable winter weather conditions in large parts of their range may benefit waterbirds (see above), and yet population trends are negative, particularly in eutrophic wetlands. Therefore, it is most likely
that other environmental and anthropogenic factors (see below) may counterbalance the positive impacts from recent years ‘favourable’ climatic conditions and drive the decline of breeding waterbirds in Finland.

Our findings support those of previous studies highlighting the deteriorating state of waterbird populations breeding in Finland (Pöysä et al. 2013, Lehikoinen et al. 2016b) and add the differential dynamics of waterbird populations in naturally eutrophic wetlands and those eutrophic wetlands surrounded by agricultural landscapes and urban areas which may be reaching a state of hyper-eutrophication. Traditionally, naturally eutrophic lakes represented a preferred habitat for many waterbirds in northern Europe, hosting higher species richness than oligotrophic lakes (Nilsson and Nilsson 1978, Kauppinen and Väisänen 1993). However, eutrophic wetlands suitable for breeding waterbirds may be disappearing in Finland and/or their quality may be deteriorating, especially those in human-dominated landscapes, therefore causing the habitat specific population declines reported here and also in previous studies (Pöysä et al. 2013, 2014, Fox et al. 2015, Lehikoinen et al. 2016b).

Although our results suggest that climate change may improve waterbird winter survival, it may also trigger a deterioration in habitat quality in northern areas. This is because increasing winter temperatures also cause an increase in rainfall, which in turn increases nutrient flow from the catchment areas of farmland landscapes (Meier et al. 2012). This phenomenon is further exacerbated by the increasing intensification of farming practices that typically implies, among others, an increased use of inorganic fertilisers, as well as autumn ploughing and removal of edge vegetation, all practices that facilitate runoff (Robinson and Sutherland 2002). The above practices, coupled with increased precipitation patterns under climate change, may ultimately boost wetland over-eutrophication. Moreover, eutrophication process may improve fish populations (Moss et al. 2011) leading into increased competition between ducks and fish (Nummi et al. 2016).

On the other hand, increasing summer temperatures may cause an increase in algal biomass and cyanobacteria, as well as in the amount of nutrients due to mineralization (Moss et al. 2011). Both of
these can lead to increasing eutrophication of wetlands, which is a symptom of severe habitat
degradation (Moss et al. 2011).

Conclusions

The importance of Finnish breeding grounds for European waterbirds is disproportionately high, with
the country supporting over half of the total European Union’s populations of several waterbird
species, such as the northern pintail, common goldeneye, Eurasian wigeon and goosander (BirdLife
International 2015). Our results, by providing new insights into the synergistic effects of drivers of
change in populations of breeding waterbirds, have important implications for the conservation of
this guild not only in Finland but throughout their entire flyway.

This finding calls for a holistic approach for conserving such an important taxonomic group. While
management actions have been proved effective in restoring wetlands for waterbirds in different
regions (Giles 1994, Ma et al. 2010, Clausen et al. 2013, Bregnballe et al. 2014), our study suggests
that these may not be enough in Finnish boreal wetlands, especially in light of future climate change.
Conservation efforts should be targeted towards landscape level management measures that would
consider the whole catchment system rather than the sole waterbody area. These efforts, however,
may still be insufficient if implemented by a single country. As our study highlights, drivers of change
in waterbird populations act at different spatial scales and some span far beyond their breeding
grounds. Ultimately, international cooperation will be key for implementing evidence-based and
effective conservation measures to ensure that habitat for waterbirds is preserved according to the
current and future conditions dictated by climate change (Pavón-Jordán et al. 2015).
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REFERENCES


Temperature does not dictate the wintering distributions of European dabbling duck species. – Ibis 155:80–88. DOI: 10.1111/j.1474-919X.2012.01257.x


abundance of wintering Eurasian Wigeon Anas penelope in northwest Europe. – Ornis Fenn. 93:12–25.


