

Waders in winter: long-term changes of migratory bird assemblages facing climate change

Laurent Godet^{1,2,*}, Mikaël Jaffré³
and Vincent Devictor⁴

¹CNRS, Laboratoire Géolittomer–UMR 6554 LETG, Nantes University, Nantes, France

²CNRS, Marine Station of Dinard–UMR 7208 BOREA, Muséum National d'Histoire Naturelle, Paris, France

³Université Lille 1, UMR CNRS 8187 LOG, Wimereux, France

⁴CNRS, UMR 5554 ISEM, Montpellier University, Montpellier, France

*Author for correspondence (laurent.godet@univ-nantes.fr).

Effects of climate change on species occupying distinct areas during their life cycle are still unclear. Moreover, although effects of climate change have widely been studied at the species level, less is known about community responses. Here, we test whether and how the composition of wader (Charadrii) assemblages, breeding in high latitude and wintering from Europe to Africa, is affected by climate change over 33 years. We calculated the temporal trend in the community temperature index (CTI), which measures the balance between cold and hot dwellers present in species assemblages. We found a steep increase in the CTI, which reflects a profound change in assemblage composition in response to recent climate change. This study provides, to our knowledge, the first evidence of a strong community response of migratory species to climate change in their wintering areas.

Keywords: climate change; waders; assemblages; community temperature index; estuaries

1. INTRODUCTION

Climate warming is unevenly distributed around the globe [1], being particularly severe in high latitudes [2]. Resident species living in high latitudes are therefore expected to suffer from a range contraction of their distribution [3]. By contrast, migratory species that breed only in high latitudes but winter in lower latitudes should have different responses to climate change, as they experience climate change unequally during their life cycle [4]. Yet, beyond changes of species ranges, the response of species breeding in high latitudes but wintering in temperate areas is still unclear.

Effect of climate change on migratory species has mainly been studied using species-by-species approaches (e.g. [5–7]). However, species responses do not necessarily correspond to the responses of species assemblages taken as a whole. In this respect,

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2011.0152> or via <http://rsbl.royalsocietypublishing.org>.

Received 8 February 2011
Accepted 3 March 2011

monitoring changes in the composition of wader assemblages provide an interesting means to investigate climate change impacts on migratory species assemblages. Indeed, in their European wintering grounds, local wader assemblages are composed of species breeding in very distinct areas, mainly (sub-)arctic regions [8]. Some of these long-distance migrants tend to winter further north in Europe, as a response to climate change [5,6]. However, the consequences of these changes at the community level remain unknown.

Here, we used wader counts over 33 years in 69 French estuaries in order to test the long-term changes in the composition of wader assemblages in response to climate change.

2. MATERIAL AND METHODS

(a) Bird data

We used the French data from the wintering wader monitoring programme conducted from 1977 to 2009 in the context of the European wetland bird survey (EWBS; electronic supplementary material, S1). Here, we considered the 23 estuarine wader species wintering in France. We further selected all French sites monitored in the EWBS, excluding Mediterranean sites, gathering populations with different migratory routes (i.e. a total of 69 sites).

(b) Community temperature index

For each species, we calculated a species temperature index (STI) (table 1) that corresponds to the mean temperature within the wintering range of the species (e.g. an STI of 5°C for a species means that the temperature averaged over the wintering range of this species is 5°C). STI was shown to be a straightforward niche metric for predicting long-term [9,10] and short-term [11] responses of bird species to climate change. STIs were obtained on a geographical information system from the overlapping of the wintering range of each species at the same time, obtained from Delany *et al.* [8] and the spatial distribution of the mean temperature in winter (averaged from 1950 to 2000 from WorldClim database: <http://www.worldclim.org>). For each species, we considered only population(s) wintering in the monitored sites (table 1).

The community temperature index (CTI) of a given assemblage corresponds to the STIs of each species within this assemblage weighted by the respective species abundances (e.g. in an assemblage 'A' composed of one individual of the species 'x' with an STI of 10°C and two individuals of the species 'y' with an STI of 20°C, the CTI will be $(1 \times 10 + 2 \times 20)/(1 + 2) = 16.67^\circ\text{C}$). In a given place, following temperature increase, we thus expect an increase in CTI resulting from the faster relative increase in abundances of individuals belonging to species with high STIs.

As waders are gregarious species and can change from very low to very high numbers locally (table 1), CTI was calculated from the log(x + 1)-transformed abundances to account for high variations in species abundances. Taking the same example as above, the CTI of the assemblage 'A' will be:

$$\frac{\log(1+1) \times 10 + \log(2+1) \times 20}{\log(1+1) + \log(2+1)} = 16.13^\circ\text{C}.$$

We also calculated CTI from the presence/absence transformed abundances (by replacing by one any species abundance exceeding one individual) to check whether the potential observed change in CTI resulted only from variation in species abundances or also from local colonizations and extinctions of individual species.

(c) Temperatures

We used the CRUTEM3 database (<http://www.hadobs.org>) to assess change in winter temperature from 1977 to 2009 (averaged from October to December) within the whole wintering area of all the studied populations. These data give the temperature anomalies using the period 1961–1990 as a reference [12].

(d) Data analysis

CTI was calculated for each site each year. Then, the temporal (year-to-year) trend in CTI was calculated with a linear model, using data from all monitored sites between 1977 and 2009. In this model, site was considered as a fixed factor and year as a continuous variable. This model thus provides the average trend in CTI, accounting for variation among sites in CTI.

Table 1. STIs, populations and subspecies of the wader species monitored in France in the context of the European Wetland Bird Survey. (Populations and subspecies wintering ranges were selected from Delany *et al.* [8]. N, Northern; S, Southern; W, Western; E, Eastern; C, Central.)

species	subspecies or populations considered in this study	STI (°C)	mean abundance per site and per year	s.e.
Eurasian oystercatcher	nominal subspecies <i>ostralegus</i>	6.850	1172.212	13.153
black-winged stilt	populations breeding from SW Europe and NW Africa	20.710	0.004	0
pied avocet	populations breeding in W Europe	12.870	362.240	6.238
grey plover	east Atlantic populations	9.490	545.090	5.205
common ringed plover	nominal subspecies <i>hiaticula</i>	4.810	219.017	1.716
little ringed plover	populations breeding from W and C Europe to NW Africa of the subspecies <i>curonicus</i>	21.620	0.002	0
kentish plover	populations breeding from E Atlantic and W Mediterranean	16.970	1.198	0.024
black-tailed godwit	subspecies <i>islandica</i>	5.140	239.081	5.666
bar-tailed godwit	nominal subspecies <i>lapponica</i>	3.870	162.575	2.117
whimbrel	subspecies <i>islandicus</i> and populations breeding from NE Europe of the nominal subspecies <i>phaeopus</i>	23.360	0.419	0.042
Eurasian curlew	nominal subspecies <i>arquata</i>	9.240	457.230	4.838
spotted redshank	European breeding populations	21.960	3.503	0.066
common redshank	subspecies <i>britannica</i> and <i>robusta</i>	3.450	103.442	1.027
common greenshank	populations breedings in NW Europe	21.790	2.518	0.038
green sandpiper	European breeding populations	14.700	1.064	0.032
common sandpiper	populations breeding in NW and C Europe	18.390	1.877	0.030
ruddy turnstone	populations breeding in NE Canada and Greenland	9.241	180.381	2.059
red knot	subspecies <i>islandica</i>	4.360	633.888	11.752
sanderling	populations breeding from Ellesmere to Taymyr and migrating/wintering in E Atlantic	10.110	189.413	2.104
little stint	populations breeding in Europe	21.240	1.848	0.048
purple sandpiper	populations breeding in N Europe and W Siberia, and populations breeding in NE Canada and N Greenland	-2.584	5.075	0.090
dunlin	nominal subspecies <i>alpina</i> ; Baltic, Britain and Ireland breeding populations of the subspecies <i>schinzii</i>	4.460	6841.790	63.926
ruff	western populations breeding from Taymyr to W Europe, and wintering from Europe to W Africa	23.720	5.251	0.210

The trend in CTI could also result from variation in the presence or abundance of only a few species rather than mirroring a real change in the composition of species assemblages. We therefore tested the robustness of the temporal trend in CTI to changes in the presence or absence of particular species. To do so, we randomly and gradually removed species from the total pool of 23 species, and calculated the trend in CTI for the remaining species (bootstrap algorithm). This was done for 1000 random removals of 1–17 species (i.e. 75% of the 23 species). If the overall trend in CTI was dependent on the dynamics of only few species, we expected to find a poor robustness of the simulated trends to the change in the species considered.

The latitudinal trend in CTI (in kilometres) was calculated with a linear model using all sites, and the mean CTI of the period 1977–2009 for each site. In this model, site was considered as a random factor and latitude as a continuous variable. Beyond the temporal (year-to-year) and the latitudinal (in kilometres) trends in CTI, a latitudinal shift of the CTI over the period (in km yr^{-1}) can be calculated using the combination of both the temporal and spatial trend in CTI [9]. Indeed, using the spatial trend ($^{\circ}\text{C km}^{-1}$) and the temporal trend in CTI ($^{\circ}\text{C yr}^{-1}$), and providing that these trends are linear, one can estimate the spatial shift in assemblage composition from the ratio of these two estimates ($^{\circ}\text{C yr}^{-1}/^{\circ}\text{C km}^{-1} = \text{km yr}^{-1}$).

The temporal trend in temperature was estimated with a linear model, using all temperature stations provided by the CRUTEM3 database that overlap the wintering range of at least one of the studied wader species. In this model, temperature station was considered as a fixed factor and year as a continuous variable.

3. RESULTS

During the period 1977–2009, the CTI increased steeply ($+0.0288^{\circ}\text{C yr}^{-1} \pm 0.0022$ s.e., $F_{1,31} = 174.4$, $p < 0.00001$, $r^2 = 0.84$; figure 1). A similar trend was found with the presence–absence data ($+0.0509^{\circ}\text{C yr}^{-1} \pm 0.0048$ s.e., $F_{1,31} = 112.1$, $p < 0.00001$, $r^2 = 0.78$; electronic supplementary material, figure S1). The trend in CTI was also highly robust to the presence or absence of particular species: it remained stable even when up to 75 per cent of the species were randomly excluded from the assemblages. Negative trend in CTI could only be observed after the removal of one-third of the species considered and most possible combinations of species were biased towards highly positive resulting trends in CTI (electronic supplementary material, figure S2).

The increase in the temperature anomaly over the same period and within the whole wintering area of the waders was highly significant ($F_{1,31} = 68.43$, $p < 0.00001$, $r^2 = 0.68$) and increased by 0.0357°C (± 0.0043 s.e.) per year (figure 1).

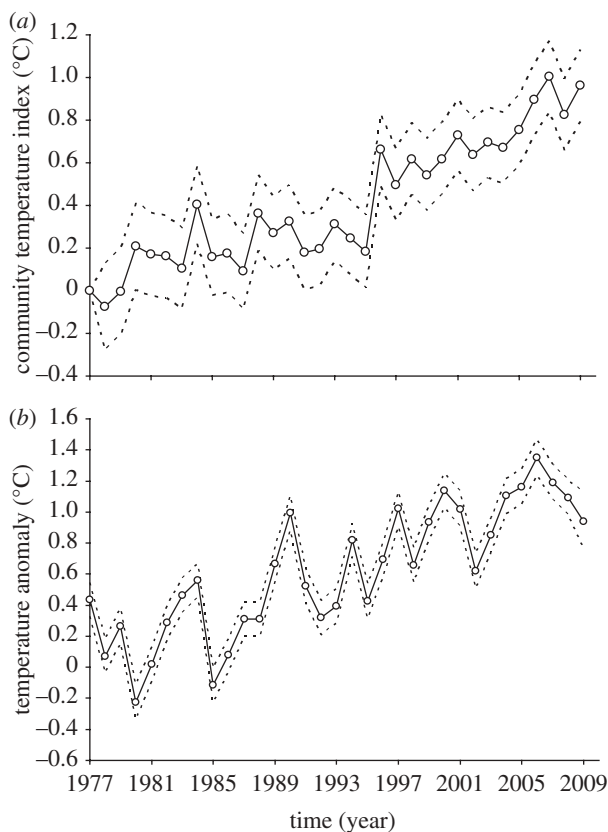


Figure 1. (a) Temporal trend of the CTI from 1977 to 2009 (first year set to zero). (b) Temporal trend of the average October–January temperature anomaly in the whole wintering area of the waders from 1977 to 2009. Dashed lines represent standard errors around the means.

CTI also significantly decreased in space from southern to northern France ($-0.0014^{\circ}\text{C km}^{-1} \pm 4.9 \times 10^{-4}$ s.e., $F_{1,67} = 8.34$, $p = 0.0052$). From 1977 to 2009, the temporal increase in CTI thus corresponded to a $20.15 \text{ km} (\pm 7.14 \text{ s.e.})$ northwards shift per year. Using presence–absence data, the spatial trend was comparable ($-0.0020^{\circ}\text{C} \pm 0.0008$ s.e. km^{-1} , $F_{1,67} = 6.69$, $p = 0.0119$) and the corresponding northwards shift in CTI was similar ($27.45 \text{ km} \pm 10.82 \text{ s.e.}$).

4. DISCUSSION

We found a consistent and important change in the composition of wader assemblages over 33 years towards species more dependent on high temperatures. This temporal trend was robust to the removal of 75 per cent of the species from the initial pool and similar when estimated with presence–absence data. These results demonstrate an important reassembly of the wader assemblages at large spatio-temporal scale on their wintering grounds.

Focusing on wintering wader assemblages provides new insights on climate change impact on bird assemblages. Not only do changes in the temperature in the breeding grounds affect the composition of bird assemblages [9], but the migratory behaviours of long-distance migratory species may also be affected by changes in temperatures in their wintering grounds.

Such changes in assemblage composition may result from different, albeit non-exclusive, mechanisms.

First, MacLean *et al.* [6] suggested that, following climate warming, young waders (that have not yet become established in favoured wintering sites) could tend to reduce their migration routes and to winter further north in contrast to adults that are site faithful to their traditional wintering grounds [13]. We can expect that these young birds predominantly belong to species with high STIs that do not have to winter in the southernmost sites anymore to thrive during very cold winters. Second, we can expect that hot dwellers (with high STIs), which are potentially more sensitive to cold temperatures, benefit more than cold dwellers from milder winters, by reducing their winter mortality to a greater extent than cold dwellers. Third, some cold dwellers (all generations pooled), which used to winter in northern France in the past, may have shifted northwards recently, and now tend to winter even further north (e.g. in the past, many oystercatchers wintered in France when tidal flats of the Wadden Sea froze over [14]). These three mechanisms could contribute to a faster relative increase in hot dweller abundance and presence in local wader assemblages, and therefore to an increase in CTI. Finally, the increase in temperature may have both direct impacts on waders (e.g. on their physiology) and indirect impacts such as changes in the abundance, distribution or accessibility of macrobenthic preys.

Maclean *et al.* [6] found a northward shift for seven wader species in Northwest Europe that was five times slower than our result. The northwards shift we found of $ca 20 \text{ km yr}^{-1}$ however, is only based on a latitudinal gradient between the southernmost and northernmost monitored French estuaries that represent a tiny part of the wader wintering range, which stretches from the Baltic Sea to tropical Africa.

This study further suggests that CTI is a suitable indicator for assessing the response of local animal assemblages to climate change. Moreover, measuring the change in assemblage composition can reveal trends that are masked at the species level. For instance, almost all wader species are increasing in France (electronic supplementary material, figure S3) and seem to be progressively shifting northwards in Europe [5,6]. However, our results suggest that different species have different dynamics within communities, which results in important changes in local assemblage compositions. In the future, because waders are among the main predators of the benthic compartment, this change in wader assemblages may have serious consequences for estuarine functions in Western Europe.

We thank volunteers involved in wader counts in France, four anonymous referees who improved this manuscript and Paul Norwood who improved the English of this text. Special thanks to Patrick Le Mao and Christophe Luczak who helped us in our data query. The authors thank Roger Mahéo who coordinated the surveys in France and the Office National de la Chasse et de la Faune Sauvage (ONCFS) that supported the monitoring and the publication of the annual reports. V.D. received financial support from the Fondation pour la Recherche sur la Biodiversité (projects FABIO and COPHY).

1 Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B. & Ackerly, D. D. 2009 The velocity of

- climate change. *Nature* **462**, 1052–1055. (doi:10.1038/nature08649)
- 2 Callaghan, T. V. *et al.* 2005 Arctic tundra and polar ecosystems. In *Arctic climate impact assessment, ACIA* (eds C. Symon, L. Arris & B. Heal), pp. 243–351. Cambridge, UK: Cambridge University Press.
 - 3 Hickling, R., Roy, D. B., Hill, J. K., Fox, R. & Thomas, C. D. 2006 The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Change Biol.* **12**, 450–455. (doi:10.1111/j.1365-2486.2006.01116.x)
 - 4 Lemoine, N., Schaefer, H.-C. & Böhning-Gaese, K. 2007 Species richness of migratory birds is influenced by global climate change. *Glob. Ecol. Biogeogr.* **16**, 55–64. (doi:10.1111/j.1466-822x.2006.00252.x)
 - 5 Austin, G. E. & Rehfisch, M. M. 2005 Shifting distributions of migratory fauna in relation to climatic change. *Glob. Change Biol.* **11**, 31–38. (doi:10.1111/j.1529-8817.2003.00876.x)
 - 6 Maclean, I. M. D. *et al.* 2008 Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Glob. Change Biol.* **14**, 2489–2500. (doi:10.1111/j.1365-2486.2008.01666.x)
 - 7 Rehfisch, M. M., Austin, G. E., Freeman, S. N., Armitage, M. J. S. & Burton, N. H. K. 2004 The possible impact of climate change on the future distributions and numbers of waders on Britain's non-estuarine coast. *Ibis* **146**, 70–81. (doi:10.1111/j.1474-919X.2004.00330.x)
 - 8 Delany, S., Scott, D., Dodman, T. & Stroud, D. 2009 *An atlas of wader populations in Africa and Western Europe*. Wageningen, The Netherlands: Wetlands International.
 - 9 Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. 2008 Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B* **275**, 2743–2748. (doi:10.1098/rspb.2008.0878)
 - 10 Jiguet, F., Gadot, A. S., Julliard, R., Newson, S. E. & Couvet, D. 2007 Climate envelope, life history traits and the resilience of birds facing global change. *Glob. Change Biol.* **13**, 1672–1684. (doi:10.1111/j.1365-2486.2007.01386.x)
 - 11 Jiguet, F., Julliard, R., Thomas, C. D., Dehorter, O., Newson, S. E. & Couvet, D. 2006 Thermal range predicts bird resilience to extreme temperatures. *Ecol. Lett.* **9**, 1321–1330. (doi:10.1111/j.1461-0248.2006.00986.x)
 - 12 Brohan, P., Kennedy, J. J., Harris, I., Tett, S. F. B. & Jones, P. D. 2006 Uncertainty estimates in regional and global observed temperature changes: a new data set from 1850. *J. Geophys. Res.* **111**, D12 106. (doi:10.1029/2005JD006548)
 - 13 Townshend, D. J. 1985 Decisions for a lifetime: establishment of spatial defence and movement patterns by juvenile grey plovers (*Pluvialis squatarola*). *J. Anim. Ecol.* **54**, 267–274. (doi:10.2307/4637)
 - 14 Camphuysen, C. J., Ens, B. J., Heg, D., Hulscher, J. B., Van der Meer, J. & Smit, C. J. 1996 Oystercatcher *Haematopus ostralegus* winter mortality in the Netherlands: the effect of severe weather and food supply. *Ardea* **84A**, 469–492.