# biology letters

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

Laurent Godet[1,2,*], Mikaël Jaffré[3]
and Vincent Devictor[4]

[1]*CNRS, Laboratoire Géolittomer–UMR 6554 LETG, Nantes University, Nantes, France*
[2]*CNRS, Marine Station of Dinard–UMR 7208 BOREA, Muséum National d'Histoire Naturelle, Paris, France*
[3]*Université Lille 1, UMR CNRS 8187 LOG, Wimereux, France*
[4]*CNRS, 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.**

## 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,

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 $(1 \times 10 + 2 \times 20)/(1 + 2) = 16.67$°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:

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

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 *ostralegus* | 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 *hiaticula* | 4.810 | 219.017 | 1.716 |
| little ringed plover | populations breeding from W and C Europe to NW Africa of the subspecies *curonicus* | 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 *islandica* | 5.140 | 239.081 | 5.666 |
| bar-tailed godwit | nominal subspecies *lapponica* | 3.870 | 162.575 | 2.117 |
| whimbrel | subspecies *islandicus* and populations breeding from NE Europe of the nominal subspecies *phaeopus* | 23.360 | 0.419 | 0.042 |
| Eurasian curlew | nominal subspecies *arquata* | 9.240 | 457.230 | 4.838 |
| spotted redshank | European breeding populations | 21.960 | 3.503 | 0.066 |
| common redshank | subspecies *britannica* and *robusta* | 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 *islandica* | 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 an N Greenland | −2.584 | 5.075 | 0.090 |
| dunlin | nominal subspecies *alpina*; Baltic, Britain and Ireland breeding populations of the subspecies *schinzii* | 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 (°C km$^{-1}$) and the temporal trend in CTI (°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 (°C yr$^{-1}$/°C km$^{-1}$ = 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°C yr$^{-1}$ ± 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°C yr$^{-1}$ ± 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).
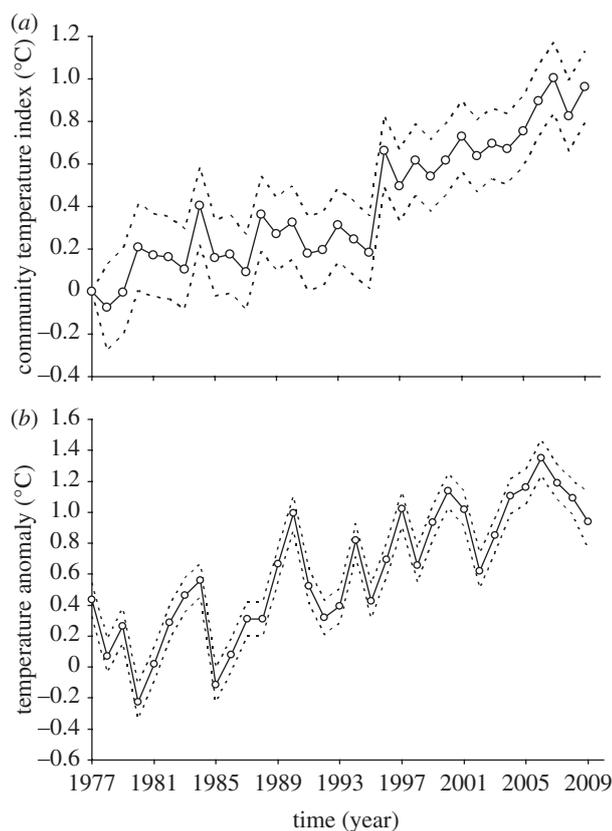
Figure 1. (*a*) Temporal trend of the CTI from 1977 to 2009 (first year set to zero). (*b*) Temporal trend of the average October–January temperature anomaly in the whole wintering area of the waders from 1977 to 2009. Dashed lines represent standard errors around the means.

CTI also significantly decreased in space from southern to northern France ($-0.0014°$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 km ($\pm 7.14$ s.e.) northwards shift per year. Using presence−absence data, the spatial trend was comparable ($-0.0020°$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 km $\pm 10.82$ 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 midler 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 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.

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