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GPS-telemetry reveals individual plasticity in the movements of Eurasian Curlews *Numenius arquata* during a cold spell

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Based on GPS tracking, we describe short-distance movements of two Eurasian Curlews *Numenius arquata* from the breeding population in northwest Germany during a cold spell that lasted about 10 days in February 2021. One bird wintering on the Dutch Wadden Sea moved towards its traditional wintering site on the Welsh coast, but stopped on the east coast of England. At the same time, another individual moved from its traditional wintering site in the Rhine-Meuse-Delta to the Bay of Veys in northern France. Such movements were not observed in the absence of cold spells in the following year. Before the movements, both birds were primarily found in coastal farmland. We suggest that the frozen soil adversely affected foraging activities of Eurasian Curlews wintering in these habitats. Our observations suggest behavioural plasticity that can enable Eurasian Curlews to withstand extreme weather events, such as cold weather.

Keywords

GPS tracking

habitat use

cold weather movement

weather conditions

shorebirds

INTRODUCTION

Environmental changes, such as alterations in weather conditions, have strong effects on bird migration. Weather conditions influence almost all aspects of migration, such as the route, duration, and timing (Berthold 2001, Elkins 2005, Klinner & Schmaljohann 2020, Bairlein 2022). Migratory patterns differ across species, conspecific populations, and even individuals of the same population (Newton 2008, Chapman *et al*. 2014, Schmaljohann 2018, Phipps *et al*. 2019, Tedeschi *et al*. 2020, Falchi *et al*. 2023). It is therefore not surprising that unusually severe weather conditions can lead to different responses in affected birds. It has been suggested that, as the weather at breeding and wintering sites is less similar for long- than short-distance migrants, the latter can adjust the timing of their migration (Butler 2003, Lehikoinen *et al.* 2004, Rubolini *et al.* 2007, Monti *et al.* 2018). Hence, short-distance migrants can be expected to be more responsive to weather conditions (Knudsen *et al*. 2011).

Unusually cold spells can be a serious problem for migrants wintering in temperate and higher latitudes (Davidson & Evans 1982, Camphuysen *et al*. 1996, Clark 2004, 2009, Newton 2007). Movements of waders related to cold weather are well known for inland-wintering species such as Northern Lapwing *Vanellus vanellus*, European Golden Plover *Pluvialis apricaria*, and Eurasian Woodcock *Scolopax rusticola*, but are less often reported in coastal-wintering waders.

We know little about effects of short-term extreme weather (Jentsch *et al.* 2007), compared with longer-term impacts of climate change (Hüppop & Hüppop 2003, Saino *et al.* 2011, Bairlein 2022). Extreme weather events can have serious consequences: in over 100 cases of such events, plant or animal populations declined by >25% and local extinctions were common (Maxwell *et al.* 2019). However, continental Black-tailed Godwit *Limosa limosa* that experienced a three-week period of low temperatures in the Netherlands in spring 2013 withstood the cold spell through migratory delays, cold-weather movements, and increasing foraging rates (Senner *et al.* 2015).

Here, we document responses of Eurasian Curlew *Numenius arquata* (hereafter Curlew) to a sudden cold spell. We studied breeding birds from northwestern Germany, which are short- and medium-distance migrants and mainly winter in nearby coastal habitats (Kämpfer *et al.* 2023). GPS-tracking has revealed high individual repeatability of departure days from the wintering grounds across years, with no relationship to weather (Schwemmer *et al.* 2021). However, this pattern does not exclude the influence of extreme weather. In our study, GPS-tagged Curlews from this population that were wintering in the Netherlands experienced an unusually cold spell for almost 10 days in February 2021. We analysed the responses of these birds in detail. This is important information for the conservation of this species, as extreme weather is increasing in intensity and frequency due to climate change (NAS 2016).

METHODS

Since 2020, we have followed the movements of 37 Curlews breeding in northwestern Germany. We deployed Ornitrack-10 solar-powered backpack tags (weight 10 g) with Global System for Mobile Communications (GSM 2G/3G; https://www.ornitela.com/). According to locations

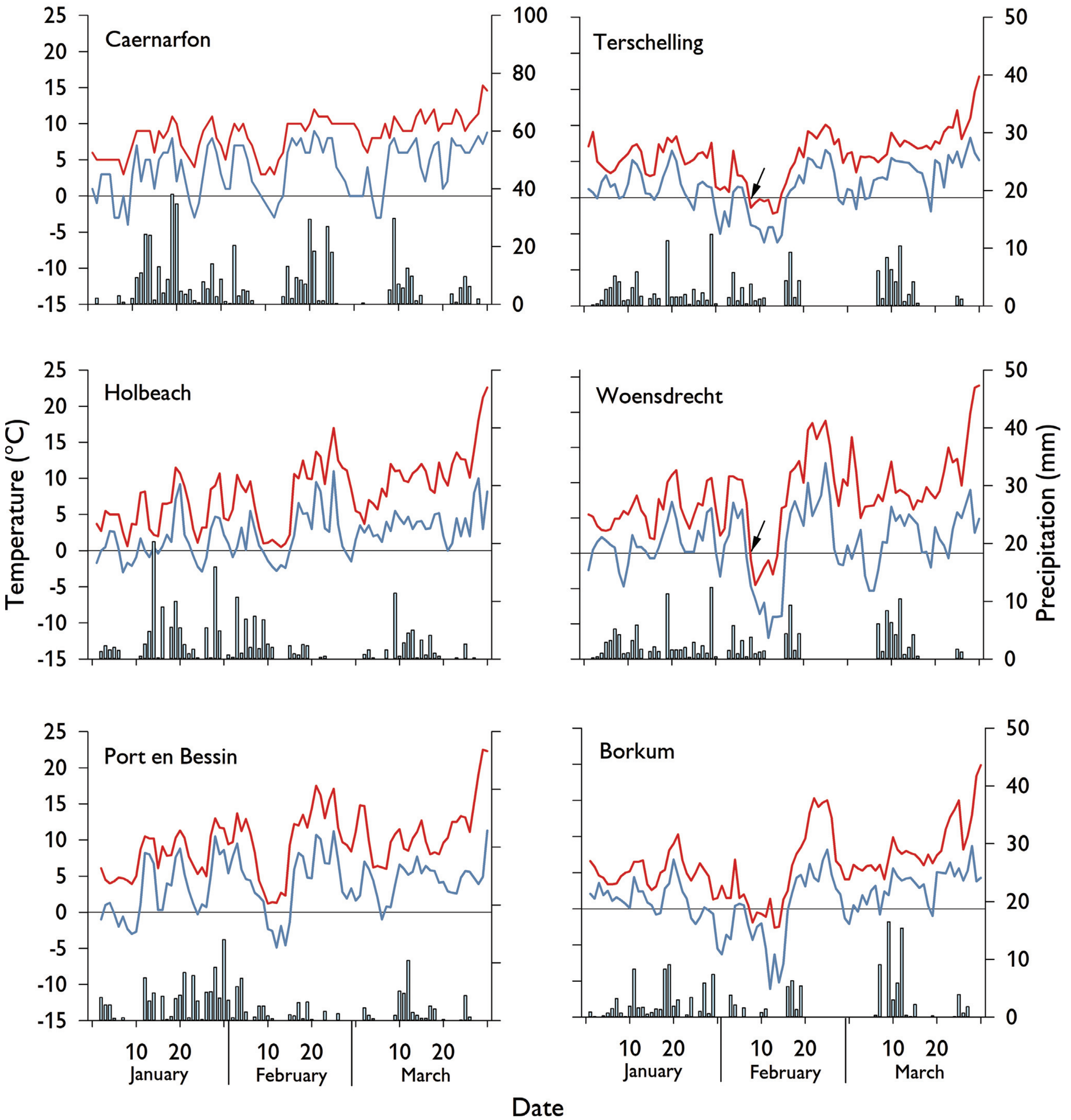

Fig 1. Precipitation (bars), and minimum (blue lines) and maximum (red lines) air temperatures between 1 January and 31 March 2021 from six weather stations in Western Europe located near wintering and stopover sites of two GPS-tagged Eurasian Curlews. Weather stations: Caernarfon (Wales, UK; 53.14°N, 4.27°W), Holbeach (England, UK; 52.80°N, 0.01°E), Terschelling (the Netherlands; 53.37°N, 5.22°E), Borkum (Germany; 53.58°N, 6.69°E), Woensdrecht (the Netherlands; 51.43°N, 4.30°E), Port en Bessin (France; 49.35°N, 0.77°W). The start of cold weather movements of the birds ID 48 and ID 18 are indicated by an arrow in the figures of the nearest weather stations (ID 48: Terschelling, ID 18: Woensdrecht).

identified by the geo fixes, most birds (n = 30) almost exclusively used intertidal wintering habitats such as mudflats, sandflats, and salt marshes. Only two individuals were found only on inland pastures, and five used both intertidal and inland habitats (*cf.* Donnez *et al.* 2023).

We caught all birds with clap-nets (80 x 90 x 45 cm with a soft net) while they were incubating. We ringed, measured, tagged, and immediately released the birds (Stroud & Davidson 2003). We used bill length to determine sex (Summers *et al.* 2013). We attached the tags with wing-loop harnesses made from teflon string and metal clips (Thaxter *et al.* 2014). In all cases, the total mass of the tag and harness did not exceed 1.8 % of body mass, which is below the recommended load limit (Kenward 2001, Bodey *et al.* 2018). We programmed the tags to record locations at five-minute intervals. In some cases (*e.g.* poor weather, short days), sunlight was not sufficient to charge the batteries. In such cases, the daily number of geo fixes was lower (range 4–286). The data were stored in the online portal Movebank (Kays *et al.* 2022).

In this paper, we focus on two Curlews that experienced a cold spell in February 2021 as a result of a negative North Atlantic Oscillation (NAO) following an early January sudden stratospheric warming (Lockwood *et al.* 2022). The cold spell occurred in northern and central Europe, with exceptionally low temperatures in Germany and the Benelux countries. Both birds experienced maximum air temperatures below zero degrees over a period of almost 10 days (8–18 Feb; Fig. 1). To relate the birds' behaviour to local weather conditions, we used online data (Lamprecht 2023) of nearby weather stations at the following sites: Caernarfon (Wales, UK), Holbeach (England, UK), Port en Bessin (France), Woensdrecht (Rhine-Meuse-Delta, the Netherlands), Terschelling (Wadden Sea, the Netherlands) and Borkum (Wadden Sea, Germany).

Roosting behaviour and roosting sites at high tide or during the hours of darkness were identified by an accumulation of geo fixes at the same place over more than 15 minutes. By contrast, geo fixes with a GPS speed of up to 1.5 m/s defined movement and those with a much higher speed and a change in location over longer distances were classified as flight. Since roosting and activity patterns of waders are often influenced by the tide in coastal regions, we also checked for high and low tide periods by using online data from the Rhine-Meuse-Delta (Bergse Diepsluis, Krammersluis; Gerding 2023) and northern France (Grandchamp; SHOM 2023). We visually checked for each day the behaviour of the tracked birds by their geo fix data and related it to the local weather conditions, the time of the day and the tide.

RESULTS

Cold weather movements

Movement back towards the wintering site – Male Curlew ID 48 experienced a sudden cold spell at a stopover site (the Wadden Sea island of Ameland) while migrating from intertidal wintering habitat on the Welsh coast to the breeding site on the German Wadden Sea Island of Borkum. The unusually cold spell with temperatures below zero at Ameland began in the evening of 6 February and lasted until 15 February. During the bird's four-day stay at inland grasslands (4–8 Feb), temperatures dropped continuously (Fig. 1). On 8 February he moved to Norfolk on the east coast of England, where he remained until 24 February (Fig. 2). On that day, when temperatures had been increasing since 15 February, the bird departed for Borkum (Table 1).

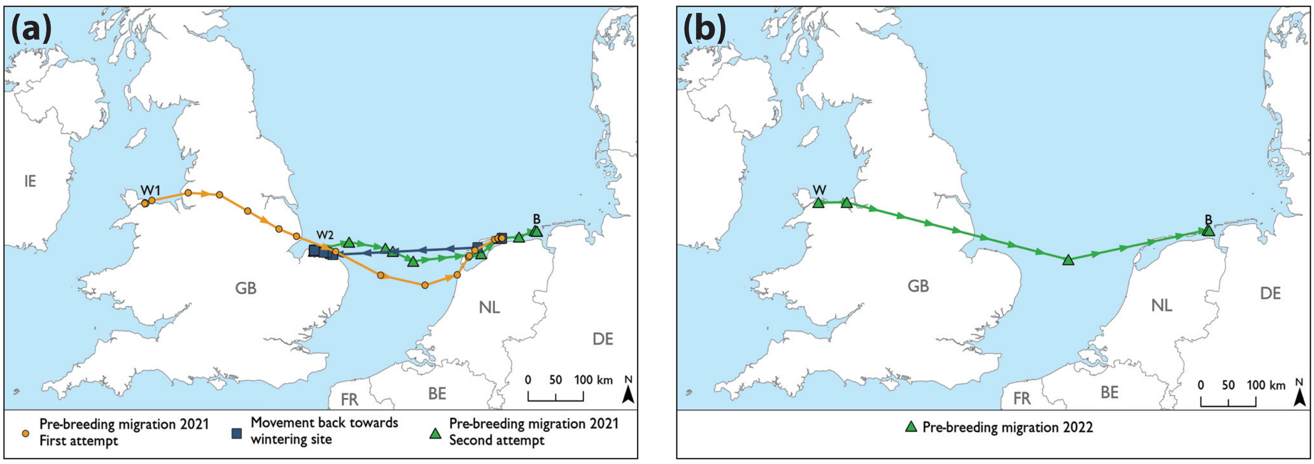

Fig 2. Migration patterns of a GPS-tagged Curlew (ID 48) in spring 2021 and spring 2022 from its traditional wintering site on the Welsh coast (W1). In 2021, the bird moved back to the east coast of England (W2, UK) during a cold spell then returned to its breeding site on the Wadden Sea island of Borkum. There was no cold-weather movement in 2022. The breeding and wintering sites of bird ID 48 are marked by B (Breeding) and W (Wintering). The symbols show the GPS-positions of the (migrating) bird before, during and after the different tracks.

Table 1. Detailed description of the cold winter movement of Curlew ID 48 in February 2021 (see also Fig. 2).

Locations	Time (UTC)	Behaviour	Temperature
From Llanfairfechan (Wales; 53.26°N, 3.99°W) to the Dutch Wadden Sea island of Texel (53.13°N, 4.93°E)	03 Feb 2021 (19:00) – 04 Feb 2021 (05:05)	Pre-breeding migration flight	8°C at departure
Mudflats near Texel	04 Feb 2021 (05:05–09:05)	Short stopover	2°C
From Texel to the Dutch Wadden Sea island of Ameland (53.45°N, 5.79°E)	04 Feb 2021 (09:05–01:00)	Continuation of the pre-breeding migration flight	2°C at departure
Ameland between the towns of Nes and Buren	04 Feb 2021 (11:00) – 08 Feb 2021 (09:05)	Foraging and resting on grasslands	The maximum temperatures declined to – 1°C in this period
From Ameland westward to the East coast of England near West Runton (52.94°N, 1.25°E)	08 Feb 2021 (06:04–04:04)	Flight back to eastern England	Maximum temperature at departure: -1°C
Farmland between West and East Runton	08 Feb 2021 (14:04) – 13 Feb 2021 (08:06)	Foraging and resting in farmland	Maximum temperatures range between 0.5°C – 2°C
Mudflats between Burnham Norton and Burnham Overy Staithe (52.97°N, 0.73°E)	13 Feb 2021 (08:06) – 24 Feb 2021 (23:40)	Foraging and resting in mudflats and marshes	Maximum temperatures increased from 1°C to 17°C in this period
From Burnham Norton eastward to the German Wadden Sea island of Borkum (53.59°N, 6.68°E)	24 Feb 2021 (23:40) – 25 Feb 2021 (11:48)	Pre-breeding migration with two short stops in the Wadden Sea to the breeding site at the island of Borkum	11°C at the start of the departure

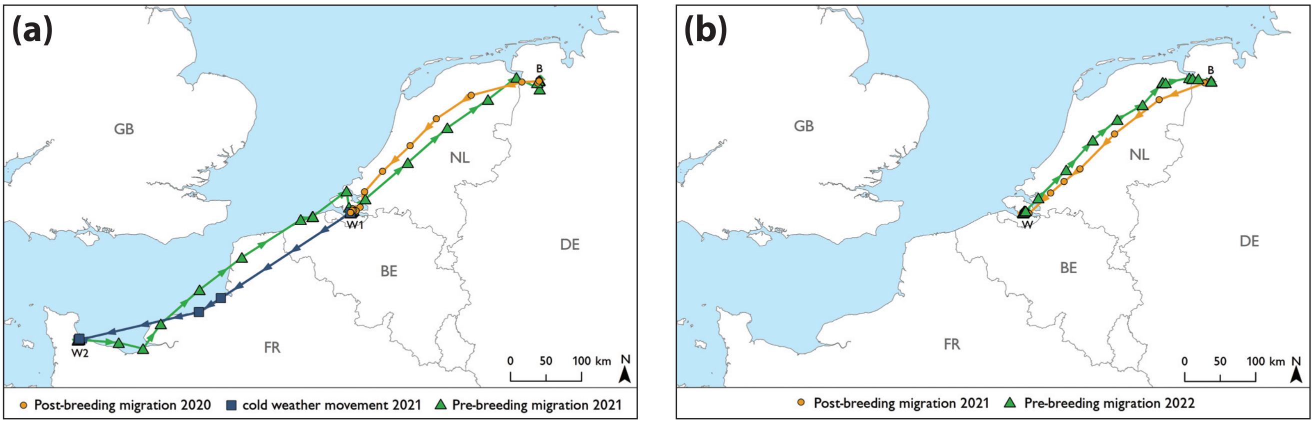

Fig 3. Post-breeding and pre-migration patterns of a GPS-tagged Curlew (ID 18) from autumn 2020 until spring 2022. In spring 2021, in unusually cold weather, the bird moved from its wintering site on the Rhine-Meuse Delta (W1, the Netherlands) to the Bay of Veys (W2, northern France). After the end of the cold spell, the bird returned to its original wintering site then departed to its breeding site at the Leda-Jümme-Niederung (northern Germany). There was no cold-weather movement in 2022. The traditional breeding and wintering site of bird ID 18 are marked by B (Breeding) and W (Wintering). The symbols refer to GPS-positions of the (migrating) bird before, during and after the different tracks.

There was no unusually cold weather in 2022, and this bird departed from the Welsh coast late on 10 February and arrived on Borkum the next morning (Fig. 2).

Southward movement from original wintering site – Male Curlew ID 18 experienced freezing temperatures at its traditional wintering site in the Rhine-Meuse-Delta (The Netherlands), which lasted almost 9 days (6–14 Feb, Fig. 1). Before his departure on 8 February 2021, he was active mainly on farmland near Bakendorp, and only used mudflats to a minor extent. He roosted mainly in the intertidal zone of the Western Scheldt but, during high tides, also roosted on nearby farmland. After moving to the Bay of Veys, France on 9 February (Fig. 3), he again was active mainly in farmland and roosted predominantly in a polder of the reserve Domaine de Beauguillot. With increasing temperatures starting mid-February (Fig. 1), he left the Bay of Veys on 22 February and made a short stopover at Uitkerke (Belgium) before returning to his original wintering site. He stayed there for another week in the same habitat as before the cold weather movement (Table 2) before moving to his breeding site late on 2 March (Fig. 3, Table 2).

Table 2. Detailed description of the cold winter movement of Curlew ID 18 in February 2021 (see also Fig. 3).

Locations	Time (UTC)	Behaviour	Temperatures
From Scheldeoord (Western Scheldt, The Netherlands, 51.39°N, 3.88°E) to Bay of Veys (northern France, 49.36°N, 1.19°W)	08 Feb 2021 (08:40) – 09 Feb 2021 (19:00)	Cold winter movement with a stopover in grasslands near Hautebut (northern France)	Temperatures below zero at the Western Scheldt since 06 Feb 2021
Coastal grasslands around the Bay of Veys	09 Feb 2021 (19:00) – 22 Feb 2021 (18:50)	Foraging and resting predominantly in grasslands	Maximum temperatures increased from 1°C to 12–17°C
From Bay of Veys to Uitkerke (Belgium, 51.30°N, 3.13°E)	22 Feb 2021 (18:50) – 23 Feb 2021 (01:00)	Pre-breeding migration to a stopover site	11°C on arrival at the Belgian coast
Grasslands west of Uitkerke	23 Feb 2021 (01:00) – 23 Feb 2021 (18:45)	Resting and foraging activities	Temperatures range between 10°–15°C
From Uitkerke to Scheldeoord	23 Feb 2021 (18:45) – 23 Feb 2021 (21:00)	Continuation of pre-breeding migration to traditional wintering site	15°C at arrival at the Western Scheldt
Farmland near Scheldeoord and Bakendorp (51.41°N, 3.90°E)	23 Feb 2021 (21:00) – 02 Mar 2021 (19:15)	Foraging activities and resting at high tides	Maximum temperatures range between 7°–19°C in this period
From Scheldeoord with two short stops to Leda-Jümme-Niederung (northern Germany, 53.22°N, 7.61E)	02 Mar 2021 (19:15) – 03 Mar 2021 (00:45)	Continuation of pre-breeding migration to traditional breeding site	1°C at the arrival

We observed no cold-weather movements by this bird in spring 2022. It left the Western Scheldt on 3 March and arrived at its breeding site in Germany the next day.

DISCUSSION

Temperate-zone wintering waders face two problems during unusually cold spells. First, they have greater energy demands (Kersten & Piersma 1987, Wiersma & Piersma 1994), and second, low temperatures reduce the density and detectability of macro-invertebrates in mudflats and the upper soil of grasslands (Goss-Custard 1969, Curry 1994, Camphuysen *et al.* 1996, Atkinson *et al.* 2003). Wintering Curlews in the Netherlands in February 2021 faced both of these challenges (e.g. the species' lower critical temperature is around 5°C; Bowgen 2017). One way to cope with sudden cold spells is to move to more favourable sites – a strategy used by inland-wintering waders such as Northern Lapwing and Golden Plover. In response to a sudden cold spell in early December 1981, for instance, the overall abundance of both species in Britain and Ireland declined rapidly which was likely a result of cold weather movements to more favourable habitats to the south (Kirby & Lack 1993). However, coastal waders are less likely to move, either remaining at their wintering sites or moving only short distances. As a consequence, mortality due to adverse weather conditions can be high in coastal waders, especially in the presence of an additional food shortage (Davidson & Evans 1982, Camphuysen *et al*. 1996, Atkinson *et al*. 2003).

In the unusually cold spell in February 2021, several observations suggested that there were cold weather movements in waders using inland habitats as wintering and stopover sites in the Netherlands and northern Germany. In particular, the maximum number of Lapwings counted by ornithologists in the Netherlands dropped by around 60% during the frost period and they moved from several inland sites (*waarneming.nl* 2023). At the same time, northern Germany experienced a large increase in Eurasian Woodcocks, which likely resulted from birds on the way to the breeding grounds in Scandinavia or further east returning to Germany (Menke 2021). Curlews of the northwest German breeding population predominantly winter along the coasts of the North Sea and the Atlantic Ocean (Pedersen *et al.* 2022, Kämpfer *et al*. 2023). However, apart from tidal habitats, wintering Curlews are also observed on coastal grasslands and inland farmland (Townsend 1981, Navado *et al*. 2013, Donnez *et al*. 2023, Pell *et al.* 2023). Unusually cold spells have led to a decline in numbers of waders in more northerly wintering habitats, e.g. the Wadden Sea, but an increase in numbers in southern coastal habitats such as the Mont Saint Michel Bay in France (Prokosch 1984, Meltofte *et al*. 1994, Le Drean-Quenec'hd *et al.* 1995, Camphuysen *et al.* 1996). In line with results of ring recoveries (Baillie *et al.* 1986) we recorded individual cold weather movements of adult Curlews in response to one unusually cold spell. As the same individuals did not move in a winter with no unusually cold spells, our findings also indicate behavioural plasticity in this species. By searching for areas that provide better foraging conditions, Curlews may be able to increase their survival probability. Another indication of individual plasticity in Curlews is that the movement of bird ID 48 did not result in a return to its traditional wintering site at the Welsh coast, where the temperatures were higher than on the East coast of

England where temperatures just above freezing when the bird arrived. This finding also indicates that the bird did not fly further than necessary to reach a suitable new wintering habitat, thus saving energy. In the search for a new wintering site moving back along the migratory pathway offers the opportunity to benefit from earlier experiences, because long-lived migratory bird species such as the Curlew should know suitable sites from former migrations.

Investigations on the occurrence of cold weather movements in the American Woodcock *Scolopax minor* revealed a sex-specific difference: males and birds in better body condition were more likely to perform cold weather movements than females and birds in poor condition (Trebilcock 2022). Interestingly, both tagged Curlews with cold weather movements in the present study were also identified as males while a tagged female bird using almost exclusively coastal farmlands in the Rhine-Meuse Delta did not move. It is possible that the females, which are larger than males, might be able to withstand lower temperatures and therefore are less likely to move when the temperature is unusually low. Alternatively, the possible sex-specific difference in the response to the unusually cold spell could be due to resource partitioning as the sexes significantly differ in bill length (*cf.* Duijns *et al.* 2014, 2015 for the Bar-tailed Godwit *Limosa lapponica*). However, due to the small sample number of tagged birds wintering in coastal farmland and faced with an unusually cold spell in the present study, it is not possible to draw a firm conclusion. Moreover, data on the sex-ratio of Curlews using coastal farmland in the Rhine-Meuse-Delta are lacking (F. Arts pers. comm.). If the habitat use of coastal farmland is male biased, as on the Wash (Pell *et al.* 2023), unusually cold spells might affect males disproportionately.

A long-term study on the effects of winter weather and the density of prey items on the wintering population of Oystercatcher on the Wash (England) indicated that the increase in mortality in some years was mainly caused by a substantial reduction in Cockles *Cerastoderma edule*, the main prey items, rather than the low winter temperatures (Atkinson *et al.* 2000). We suggest that it is not the low temperatures but the frost-induced change in feeding conditions that are decisive for movements of some wintering Curlews in the present study. Most of our GPS-tagged Curlews remained at their traditional wintering sites and a resident bird breeding on the Wadden Sea island of Spiekeroog showed no cold weather movement during the cold spell in February 2021 (Kämpfer *et al.* 2023). Additionally, we recorded cold weather movements only in two birds which mainly foraged in coastal farmland. It is likely that the foraging activities of these Curlews had been adversely affected by the cold spell because the topsoil of fields was frozen, which makes soil macroinvertebrates inaccessible (but note the small sample size). By contrast, we suppose no such problems in the mudflats of the intertidal zone due to both salinity and the temperature of the water (see Bing & Ma 2011). However, the food supply harvestable by waders in the intertidal zone depends on a variety of factors including a reduction in available prey through the winter (Wanink & Zwarts 1993, Zwarts & Wanink 1993).

Extreme weather events are well known to affect population dynamics. Waders may die in unusually cold spells (see Clark 2004), if they are unable to adapt by behavioural responses, e.g. cold weather movements or increasing foraging rates during the frost period. With regard to the latter, migrating Black-tailed Godwits were found to withstand the consequences of an extreme cold spell in this way (Senner *et al.* 2015). Similar results have been obtained for the Curlew in the present study.

Curlews are able to switch immediately from grasslands and arable fields to intertidal habitats and *vice versa* (Donnez *et al.* 2023, Summers & Kalejta-Summers 2023). However, in the present study, both tracked Curlews wintering in farmland habitats continued to feed inland even in an unusually cold spell instead of moving to nearby coastal habitats. With regard to the underlying mechanism, we can think of different factors which might not be mutually exclusive: (1) The overall biomass of the macrobenthos in winter is half of that in summer and burying depth of several species is deepest in midwinter (Esselink & Zwarts 1989, Zwarts & Wanink 1993). Thus, limitation in food supply might stop the birds switching from farmland to nearby mudflats; (2) According to behavioural studies in the non-breeding season, approximately 20% of the Curlews defend feeding territories on the mudflats at the Frisian Coast of the Dutch Wadden Sea (Ens & Zwarts 1980, Ens 1983). In the Beauly Firth (northern Scotland) over 70% of the Curlews defended small, single-ownership intertidal territories at low tide (Summers 2019, Summers & Kalejta-Summers 2023). Winter territoriality of resident Curlews in the intertidal mudflats might have discouraged inland-wintering birds in the Rhine-Meuse-Delta from using these nearby habitats. Winter territoriality might also be a factor influencing the habitat use of bird ID 18 after its cold weather movement to northern France. When the bird arrived at the Bay of Veys, high densities of Curlews at the mudflats might have forced it to restrict its activities to adjacent coastal farmland (P. Bocher pers. comm.).

Although extreme weather events can arise throughout a year, they might especially affect bird and mammal species in winter, when food resources are scarce and thermoregulatory costs are high. Thus, for a lot of species the winter already represents energetic bottlenecks which might make them vulnerable to extreme weather events like unusually cold spells. With regard to the present study, we found evidence that due to behavioural plasticity Curlews can withstand such cold spells via movements to more favourable sites.

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