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When Siberia came to the Netherlands: the response of continental black-tailed godwits to a rare spring weather event

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Summary

1. Extreme weather events have the potential to alter both short- and long-term population dynamics as well as community- and ecosystem-level function. Such events are rare and stochastic, making it difficult to fully document how organisms respond to them and predict the repercussions of similar events in the future.

2. To improve our understanding of the mechanisms by which short-term events can incur long-term consequences, we documented the behavioural responses and fitness consequences for a long-distance migratory bird, the continental black-tailed godwit *Limosa limosa limosa*, resulting from a spring snowstorm and three-week period of record low temperatures.

3. The event caused measurable responses at three spatial scales – continental, regional and local – including migratory delays (+19 days), reverse migrations (>90 km), elevated metabolic costs (+8.8% maintenance metabolic rate) and increased foraging rates (+37%).

4. There were few long-term fitness consequences, however, and subsequent breeding seasons instead witnessed high levels of reproductive success and little evidence of carry-over effects.

5. This suggests that populations with continued access to food, behavioural flexibility and time to dissipate the costs of the event can likely withstand the consequences of an extreme weather event. For populations constrained in one of these respects, though, extreme events may entail extreme ecological consequences.

Key-words: behavioural flexibility, carry-over effects, migration, resource availability, stress response

Introduction

The fitness of individual organisms depends in large part on their ability to adequately respond to changes in their environment – including both short-term perturbations such as weather-related events and long-term change such as habitat alteration or loss. While the consequences of long-term environmental change are well appreciated, the effects of short-term perturbations are poorly understood (Jentsch, Kreyling & Beierkuhnlein 2007). Those studies that have

focused on short-term perturbations have found they can be separated into two classes: (1) severe and (2) extreme (*sensu* Smith 2011). Although severe events have relatively limited consequences, extreme events have considerable and lasting effects, especially on plant and lower trophic level communities (Niu *et al.* 2014). In some cases, even higher trophic level communities can experience dramatic repercussions. For instance, the passage of a 10 000 km² iceberg through the Antarctic Ross Sea caused short-term reproductive failure and higher long-term variability in reproductive rates in emperor penguins *Aptenodytes forsteri* and Weddell seals *Leptonychotes weddellii* (Kooyman *et al.* 2007; Chambert, Rotella & Garrott 2012). Some of the

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most well-known examples of evolutionary change occurring over ecological time-scales, such as in Darwin's finches *Geospiza* sp. and cliff swallows *Petrochelidon pyrrhonota*, have also followed populations in the wake of extreme events (Grant & Grant 1993; Brown & Brown 1998). These studies remain few, however, and there is still much to learn about how both severe and extreme events can affect organisms, especially while they are occurring (Breuner, Delehanty & Boonstra 2013).

Determining the full extent of a population's response to such weather events is difficult to accomplish: severe and extreme events are rare and occur stochastically, making it impossible to plan for their occurrence. Most studies addressing the consequences of these events therefore do so *post hoc*, as one aspect of a longer-term population-level study (e.g. Zhou *et al.* 2013). Other studies instead only focus on within-season population-level effects, rather than individual and long-term responses (e.g. Bonter *et al.* 2014). Those studies that do succeed in documenting the responses of individuals to such weather events as they occur have largely focused on the potential for severe events to drive short-term physiological and behavioural changes through the induction of stress responses (de Bruijn & Romero 2011). While triggering a stress response can induce behaviours as varied as increased foraging rates and short-distance migratory movements (Hahn *et al.* 2004; Metcalfe *et al.* 2013), these studies suggest that individual responses to severe events have limited scope and few fitness consequences (Breuner, Patterson & Hahn 2008; Crespi *et al.* 2013). In contrast, coverage of extreme events and their direct effects on animal behaviour is largely lacking (cf., Kooyman *et al.* 2007), making it difficult to predict how organisms should be expected to respond to extreme events and how these responses might differ from those induced by severe events. To fill this gap, it is necessary to combine behavioural studies of individuals that identify their responses to severe and extreme events with longer-term studies that detail the resulting fitness consequences and their impacts on population dynamics.

Understanding how organisms respond to severe and extreme events has broader applications as well. For instance, climate models predict the frequency and severity of weather events will increase in the coming century (Meehl & Tebaldi 2004), suggesting that detailing how organisms respond to stochastic weather events may become critical to our ability to conserve threatened populations (Ovaskainen & Meerson 2010). Additionally, while severe and extreme weather events may be rare, the physiological and behavioural responses they induce are not unique (Wingfield, Kelly & Angelier 2011). For many individuals, the line between coping with and succumbing to a stressor may be narrow, meaning that our ability to identify those circumstances that stress individuals in a population – no matter the cause – and the manner in which they dissipate the costs imposed by those stressors can have far-reaching implications (Senner *et al.* 2014).

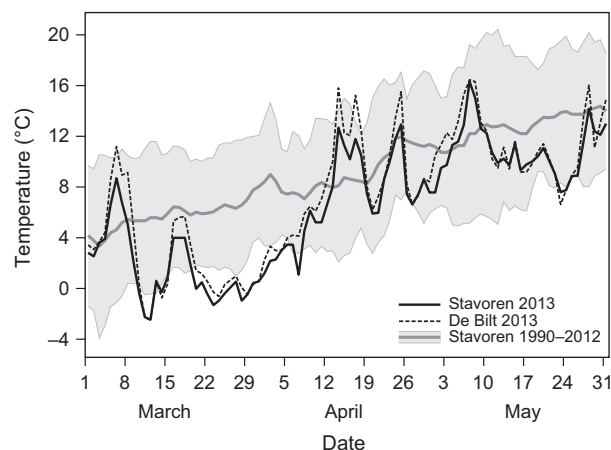


Fig. 1. Spring temperatures in Stavoren and De Bilt, the Netherlands 1990–2013. The black line represents daily mean temperatures in Stavoren in 2013; dotted black line daily mean temperatures in De Bilt in 2013; dark grey line daily mean temperatures in Stavoren from 1990 to 2012; and light grey shaded area 2 standard deviations from mean daily temperatures in Stavoren from 1990 to 2012.

Here we present data on the response to a rare weather event by a long-distance migratory bird, the continental black-tailed godwit *Limosa limosa limosa* (L.; hereafter, godwits), both during the course of the event and over two subsequent breeding seasons. That event occurred in March 2013, when temperatures plummeted more than 10 °C across Western Europe over a two-day period, pre-saging a snowstorm that left half a metre of snow as far south as central France, three weeks of record and near-record low temperatures, and two months of below average temperatures (Fig. 1; Royal Dutch Meteorological Institute 2014). This event overlapped with peak godwit migration and arrival at breeding sites, thus presenting an excellent opportunity to document their response to a stochastic weather event and detail the consequent repercussions.

In order to document the full range of their response to the event, we tracked individual godwits at three spatial scales ranging from the continental to the local. We then determined the short-term (i.e. direct effects; Breshears *et al.* 2005) and longer-term consequences (i.e. carry-over effects, *sensu* Harrison *et al.* 2011) of their responses and identified whether those consequences led to alterations in population-level dynamics. We show that, although this weather event was considered extreme by meteorological standards and did induce a variety of responses with real physiological costs, the long-term consequences were limited and contrary to expectations.

Materials and methods

STUDY SPECIES

Continental black-tailed godwits breed across Europe, but at least 80% of the East Atlantic flyway population nests in the

Netherlands (Thorup 2005). During the non-breeding season, most birds reside in sub-Saharan Africa – especially Senegal, Mauritania and Guinea Bissau – while the rest remain in Iberia, predominantly on the southern coasts of Spain and Portugal (Hooijmeijer *et al.* 2013). Northward migration progresses in stages, with those birds spending the non-breeding season in West Africa moving to the Iberian Peninsula starting in late December and remaining there for >90 days (Lourenço *et al.* 2010; Masero *et al.* 2011). In March, most godwits move northward again, with departures from Iberia peaking 10–20 March. After departing Iberia, some individuals may additionally stop in France, Belgium and the south-western Netherlands before arriving at breeding sites (Lourenço *et al.* 2011). Arrivals at Dutch breeding sites in the province of Friesland begin in early March and extend into April, but most birds arrive 20 March to 1 April (Lourenço *et al.* 2011). The interval between arrival at breeding sites and clutch initiation can approach five weeks for many godwits ($\bar{x} = 35 \pm 16$ days; this study). The bulk of this time is spent on or near nesting territories, and daily activities are largely comprised of foraging, territory acquisition and defence, and rest, with longer movements away from breeding territories undocumented (van den Brink *et al.* 2008). Average initiation date of first nests in Friesland is the first week of April, with the peak occurring 15–20 April (Schroeder *et al.* 2012).

FIELD EFFORTS

To assess the range of responses displayed by godwits to the weather event, we combined data from a range of sources – some coincidental, some planned and some enabled by our long-term godwit study in Friesland, the Netherlands (e.g. Kentie *et al.* 2013, 2014). Together, these data sources allowed us to follow individual godwits at the continental, regional and local scale and to integrate their behaviour across all three. Our data collection is detailed here separately for each spatial scale.

Continental

Between 30 January and 2 February 2013 and 31 January and 18 February 2014 near the town of Hernan Cortes, Spain (5-9112° W, 39-0364° N) – within the core Iberian staging area (Masero *et al.* 2011) – we used mist nets at nocturnal roost sites to capture 30 adult female godwits for outfitting with satellite transmitters. Solar-powered PTT-100s (9.5 g) from Microwave Technology Inc. were attached using a leg-loop harness made of 2 mm nylon rope; in total, the attachment weighed ~12 g, leading to an average loading factor of $3.43 \pm 0.22\%$ of an individual's mass at the time of capture. To ensure that these individuals could acclimate to the transmitter attachment, they were kept for two nights in aviaries at the Universidad de Extremadura (Badajoz) and then released near the original capture site during daylight hours. Transmitters were programmed to transmit for 10 h and recharge for 48 h, which allowed enough contact to identify migratory stopovers used for >2 days. All location fixes were retrieved via the CLS tracking system (www.argos-system.org) and passed through the Douglas Argos-filter (DAF) algorithm (Douglas *et al.* 2012). Standard class locations (i.e. LC 3, 2, 1) were retained and auxiliary class locations that did not meet our pre-defined thresholds for maximum movement rate (120 km h^{-1}) and spatial redundancy (10 km) excluded using the hybrid filtering method in the DAF. This resulted in 44 ± 5 ($n = 30$) filtered

locations per individual per year that were used to quantify spring movements (10 February to 31 May).

Regional

Since 2003, >8000 godwits have been marked with individually unique colour combinations or coded flags in a coordinated scheme (Cidraes-Vieira 2013). This has allowed for the creation of a volunteer-based, large-scale resighting effort covering much of continental Europe (e.g. Alves *et al.* 2013). During northward migration in 2013 and 2014, we collated all resightings of colour-marked godwits collected between staging sites in Iberia and breeding sites in the Netherlands to document the migratory patterns of individuals with known breeding locations.

Local

Since 2004, we have carried out a landscape-scale demographic study in one of the core godwit breeding areas in Friesland, the Netherlands (Groen *et al.* 2012). Our study area has grown over time. From 2004 to 2006, it encompassed only 400 ha (Lourenço *et al.* 2011), but was expanded to ~8000 ha in 2007 (Kentie *et al.* 2013) and again to ~10 000 ha in 2012, so that it now extends from the village of Makkum (53-0672°N, 5-4021°E) in the north, to Laaksum (52-8527°N, 5-4127°E) in the south and Woudsend (52-9432°N, 5-6285°E) in the east. Despite the growth in size, research effort per unit area has changed little so that the data collected remain broadly comparable.

From 2005 to 2014, the demographic study area was searched daily throughout the pre-laying phase for colour-marked individuals, from the arrival of the first adult until the initiation of the first clutch. Additionally, once each week (2009–2010, 2012–2014), every field was surveyed for the presence of godwits – marked or unmarked – and every individual observed categorized as either territorial or non-territorial, based on behavioural cues (Kentie *et al.* 2014). Combined, these gave us annual arrival dates and resighting histories for individually colour-marked godwits and a season-long phenology of godwit breeding behaviour at the landscape scale.

In 2013, we initiated an intensive study of godwit reproductive biology in the 220-ha Haanmeer Polder (52-9226°N, 5-4336°E), which is nested within our larger demographic study area. In the Haanmeer, we made repeated observations of colour-marked females to ascertain whether females increased their foraging rates in response to the weather event (8 March–17 April). For these females, we recorded their foraging rates – the number of probes, which we defined as a downward movement of the bill into the soil, and successes, which we defined as a swallowing motion (Senner & Coddington 2011) – during 10 consecutive 3-min periods, for a total of 30 min of foraging observations per bird per day during daylight hours. Only observations resulting from complete 3-min periods are reported here.

Beginning in early April, the entire study area was searched for nests. Upon discovery, nest coordinates were recorded and, if/when a clutch was complete, its eggs floated to determine lay date (Liebezeit *et al.* 2007) and measured to assess egg volume (Schroeder *et al.* 2012). To determine nest fates, nests were visited once every 3 days (Haanmeer) or a week prior to hatch and thereafter regularly until hatch or depredation (demographic study area; see Kentie *et al.* 2015). Throughout the entire study area, an effort was also made to connect colour-marked adults to nests.

After hatch, within the Haanmeer, we attempted to locate all colour-marked parents to assess the fledging success of their broods. Godwit chicks begin fledging at 25 days (Kruk, Noordervliet & ter Keurs 1997), and daily surveys for colour-marked adults began 25 days after the first nests hatched. If a family (i.e. either adult) was not encountered on the first day of its fledging period, we searched for it the following 2 days; if a family was not observed for 3 days, the brood was considered to have failed. No effort was made to determine the number of chicks fledged by each family, as reliably relocating precocial chicks without the aid of radiotransmitters is exceedingly difficult (e.g. Kentie *et al.* 2013).

WEATHER DATA

To quantify the conditions experienced during the weather event, daily weather data (1 March – 1 June) were obtained from the Royal Dutch Meteorological Institute's data base (www.knmi.nl) for two locations: Stavoren (52.8829° N, 5.3607° E), a weather station located within our study area in Friesland, and De Bilt, Utrecht (52.1000° N, 5.1833° E), the closest weather station to the centre of the region to which we tracked reverse migrating godwits. For each site, daily measurements were acquired for minimum, maximum and mean temperatures; mean wind speed; and total precipitation. For comparison to historical conditions, the same data were obtained from Leeuwarden (53.2231° N, 5.7157° E) for 1951 to 1989 and Stavoren for 1990 to 2014 (the period for which data were available).

STATISTICAL ANALYSIS

Differences in migratory patterns

Using satellite telemetry data, we documented departure dates from non-breeding sites, duration and location of stopover sites, and arrival dates at breeding sites to compare differences in migratory patterns between 2013 and 2014. Departure from non-breeding sites occurred when an individual moved ≥ 25 km north from the centre of its non-breeding area, stopovers when an individual's movements were ≤ 25 km over the course of one duty cycle after the onset of migration, and arrival at breeding sites when an individual had arrived to an area ≤ 25 km from its final nesting location as corroborated by on-the-ground observations; stopover duration was the length of time between the first and last location fixes from each stopover site. Because of transmitter duty cycles, all estimates of departure and arrival dates and stopover durations are approximate, but likely accurate to within 1–2 days. The locations of stopover and breeding sites were determined by calculating the mean latitude and longitude of all filtered location fixes collected during an individual's stay in an area.

Because our sample size of repeated migration tracks was limited, we made comparisons between years using those individuals only tracked during 2013 ($n = 7$), those tracked during both 2013 and 2014 ($n = 8$) and those individuals only tracked in 2014 ($n = 15$). To do this, we used linear mixed-effect models with individual as a random effect and year as a fixed effect to compare departure dates from non-breeding sites in Spain, the number of stopovers made during northward migration, the duration of those stopovers and arrival dates at breeding sites. Because conditions were relatively colder farther north in Europe in 2013

(Royal Dutch Meteorological Institute 2014), breeding latitude was included as a covariate to identify potential differences in migratory patterns caused by the deterioration of conditions at higher latitudes.

In all analyses, predictor variables were standardized across all years (Gelman 2008). We then used a candidate model approach, in which we tested each fixed effect separately, as well as all potential combinations among them, with the model with the lowest AIC_c score – to account for small samples sizes – chosen as the most well-supported model (Burnham & Anderson 2002; Arnold 2010). If no one model had a model weight (w_i) > 0.90 , we identified the most important predictor variables through a model averaging process (Grueber *et al.* 2011). All models were run using the 'lme4' (Bates *et al.* 2014) and 'AICcmodavg' (Mazerolle 2011) libraries in Program R (Version 3.0.2; R Development Core Team 2013).

Migratory anomalies

Our resighting data base was used to determine whether the weather event incurred any migratory anomalies, such as reverse migration or vagrancy. Reverse migrations occurred when an individual was first observed at our breeding site in Friesland and subsequently resighted at sites south of the study area prior to the onset of the laying phase; vagrancy when an individual was observed outside those migratory paths delimited by our satellite telemetry data (i.e. longitudes 6°W – 6°E) during this same period, regardless of whether it had already been observed in the study area that spring. To minimize the number of false reports, observations of godwits with low confidence scores were excluded – that is when an individual's rings were reported as discoloured or its identity uncertain. Finally, to ascertain the potential energetic costs of abnormal movements, we calculated the great circle distance between an individual's breeding site in south-west Friesland and the furthest location from which it was reported during its ensuing movements.

Spectrum of behavioural responses

Initial analyses of movement data and colour-ring resightings suggested three distinct behavioural responses to the weather event – on-time arrival and persistence at breeding sites throughout the event; delayed arrival at breeding sites; and reverse migrations. We quantified the proportion of the breeding population at our study site employing these three behaviours, as well as one other likely behaviour – normally late-arriving individuals that may have missed the coldest conditions altogether.

Given the imperfect coverage of all sites potentially hosting godwits, reliance on resightings alone would significantly underestimate the total number of individuals undertaking reverse migrations. Thus, using our observations in Friesland, daily resighting histories were generated for all colour-marked godwits observed within the study area prior to the initiation of the first clutch on 18 April. Then, using those individuals for whom reverse migratory movements were verified by on-the-ground sightings, we determined the duration of reverse migrating individuals' absences from the study area. Using the minimum absence recorded, individuals with longer absences, but no resightings outside of the study area were identified and labelled as possible reverse migrants; individuals with shorter absences were denoted as a third group – those that stayed in the study area. Finally, we

used a Cormack-Jolly-Seber (CJS) model in RMark (version 2.1.9; Laake 2014), coupled with a goodness-of-fit test in U-CARE (version 2.3.2; Choquet *et al.* 2009), to determine whether the resighting histories of these three groups were statistically distinguishable from one another. For this, the survival probability (S) was fixed to 1, but the resighting probability allowed to vary by group and time across the duration of the weather event (6 March–18 April).

We then distinguished individuals that delayed their arrival from individuals that normally arrive late to the breeding grounds. To do this, we used the arrival date histories from 2004 to 2012 for all individuals resighted within the study area in 2013 prior to initiation of the first clutch on 18 April to determine each individual's mean historical arrival date and the standard deviation among its previous arrival dates. Then, we calculated whether an individual's arrival in 2013 was more than two standard deviations after its previous mean arrival date using its individual arrival date standard deviation; individuals with only one previous arrival date were assigned the population mean standard deviation ($\bar{x} = 7 \pm 5$ days). If an individual arrived after 1 April, but not its individually specific late arrival date, it was instead identified as 'normally late'. Individuals marked for the first time in 2012 – and thus with no arrival date history – or only observed once during the study period were excluded from all analyses.

Short-term consequences

One potential difference among response strategies was the energetic cost of reverse migration versus remaining on the breeding grounds during the period of low temperatures. To determine this cost, we first averaged the great circle distances flown by all individuals observed undertaking reverse migrations. Next, using Program Flight (version 1.24; Pennycook 2008), we calculated the energetic cost of a round trip flight of this distance, parameterized with measurements from Alves & Lourenço (2014). Then, with daily weather conditions – temperature and wind – obtained from the De Bilt weather station, we used equation 2 from Cartar & Morrison (1997) to estimate an individual's maintenance metabolic rate (MMR) in watts (W) based on environmental conditions. Using our MMR estimates, the daily metabolic expenditures of a reverse migrating individual were compared with those of an individual staying in Friesland using a linear model with behavioural response type as a fixed effect. As a final measure, a reverse migrating individual's daily metabolic output was summed with the cost of the two-way migratory flight (from Program Flight) and compared to the summed daily MMR values of an individual staying in Friesland.

Next, we explored how females remaining in Friesland met the costs of residency. For this, we compared daily mean foraging and success rates averaged across individuals using linear models. Date, the current day's minimum temperature, total precipitation and mean wind speed were included as predictor variables. [Neither individual, time of day, nor foraging location significantly affected foraging rates (M.A. Verhoeven & N.R. Senner, unpublished data).]

Longer-term consequences

The final step in our analysis was to determine whether the costs of the pre-laying phase carried over to the breeding season and beyond. To do this, we compared return rates and reproductive

parameters for all individuals across years of our long-term study and among individuals exhibiting the four response strategies. For comparisons across years, we determined the number of individuals observed during the pre-laying phase in each year and the proportion of those individuals returning the following year (2005–2014). The number of parcels occupied by territorial pairs present across the study area was also quantified (2009–2010, 2012–2014); as were mean lay dates, egg volume and clutch size of all nests; and rates of nest abandonment, nest survival and fledging success (2013–2014). We analysed daily nest survival (DSR) rates in Program MARK using known fate nest survival models (Dinsmore, White & Knopf 2002; see Kentie *et al.* 2015 for more details). All other data were analysed using generalized linear or logistic mixed models with year as a fixed effect and individual as a random effect (where appropriate); sex – as determined by genetic sexing (Schroeder *et al.* 2010) – was also included as a fixed effect in analyses of return rates. In order to determine whether 2013 and 2014 differed from previous years, each model was run twice, once with 2013 as the reference year and once with 2014 as the reference year. These same metrics – using the proportion of birds identified as nest associates instead of the peak number of parcels occupied as a proxy for breeding propensity – were compared among individuals exhibiting the four response strategies within 2013 and 2014 using generalized linear or logistic mixed models with behavioural response type and year as fixed effects and individual as a random effect; only females were included in analyses of lay date, clutch size and egg volume.

Results

CONTINENTAL SCALE MOVEMENTS

We tracked 14 and 23 individuals for their entire northward migrations in 2013 and 2014, respectively, and 8 individuals in both years. Of these individuals, 12 and 16 migrated to breeding sites in continental Europe; the remaining individuals either did not migrate ($n = 2$ & 6) or migrated to Iceland, indicating they belonged to the Icelandic subspecies, *L. l. islandica* ($n = 1$ & 1). All *L. l. limosa* godwits bred either in the Netherlands ($n = 25$), Belgium ($n = 1$) or Germany ($n = 2$), between 50.97–53.85°N and 2.70–8.39°E.

In 2013, godwits departed Iberia on 13 March \pm 3 days ($n = 12$), made an average of 1.8 \pm 1.6 stops ($n = 12$) for 7 \pm 4 days ($n = 12$), and arrived at breeding sites on 31 March \pm 12 days ($n = 12$; Fig. 2). In 2014, the average departure date was 17 March \pm 3 days ($n = 23$), and individuals made 1.3 \pm 1.1 stops ($n = 23$) for a total of 6 \pm 4 days ($n = 23$), before arriving at their breeding sites on 27 March \pm 14 days ($n = 23$; Fig. 2). In no case did the model averaging process identify a variable as biologically relevant, and in all cases, the null model was the lowest AIC_c model (Tables S1 and S2, Supporting information). Although in two cases – for the models testing the relationship between year and departure date (Δ AIC_c = 1.62, $w_i = 0.31$) and year and the number of stops made (Δ AIC_c = 0.40, $w_i = 0.29$) – the second most well-supported model had a similar AIC_c score (i.e. <2 Δ AIC_c),

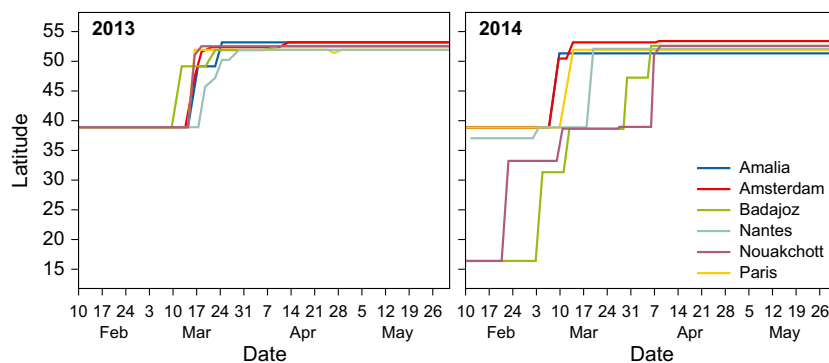


Fig. 2. Northward migration timing of black-tailed godwits ($n = 6$) tracked with satellite telemetry devices in both 2013 and 2014. Coloured lines represent the latitude of individual godwits by date. All individuals were initially captured in Extremadura, Spain in February 2013.

the additional parameters included in these models were uninformative (Table S1). While our sample size was too small to perform statistical tests among only those godwits that were tracked and migrated northward both years ($n = 6$), individuals departed later ($+5 \pm 12$ days), stopped less frequently (-1 ± 1 stops), for a longer period of time ($+4$ days), arrived earlier (-2 ± 12 days) and spent less time migrating (-7 ± 9 days) in 2014 (Fig. 2).

REGIONAL SCALE MOVEMENTS

In 2013, we observed 324 individuals in our Frisian study area prior to 1 April. Of these, 39 individuals were subsequently resighted at locations south of our study area (Fig. 3), with all observations reported from either Belgium ($n = 2$) or the Netherlands ($n = 37$). On average, individuals moved 91.7 ± 39.0 km and were absent from the study area for 22 ± 12 days ($n = 39$). We observed no godwits exhibiting vagrancy in 2013 and neither vagrancy nor reverse migratory movements in 2014.

RESPONSE STRATEGIES

In 2013, we observed a total of 591 colour-marked individuals in our study area prior to the onset of the laying phase. Using individual resighting histories, we identified 224 godwits that likely made reverse migrations and were absent from the study area for 17 ± 8 days. The resighting probability of these individuals during the pre-laying phase was indistinguishable from that of individuals resighted south of the study area ($\hat{c} = 1.66$; $w_i = 1.00$; Tables S3 and S4, Supporting information). Thus, when combined with those individuals physically observed south of the study area, a total of 263 birds made reverse migrations after arriving in Friesland. The remaining 61 individuals arriving in Friesland prior to 1 April spent the entire period in the study area. For this group, the longest duration between resightings was 3 ± 1 days ($n = 61$). An additional group of 267 godwits were first seen in the study area between 1 and 17 April. Of these, 66 were individuals normally first observed after 1 April, 99 individuals that probably delayed their arrival, and 101 individuals marked in 2012. Individuals that delayed their migrations arrived 20 ± 6 days ($n = 99$) later than their previous

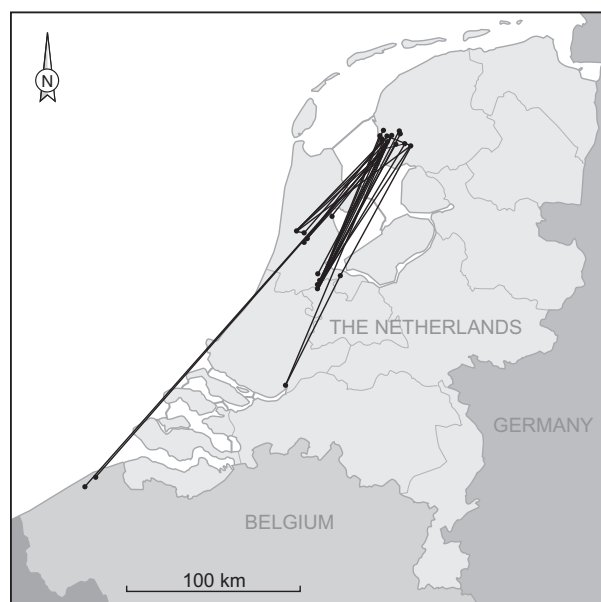


Fig. 3. Reverse migratory movements of colour-marked black-tailed godwits ($n = 39$) breeding in Friesland, the Netherlands during March and April 2013. All lines represent movements of individual birds from the demographic study area in Friesland – where they were initially observed – to areas to the south – where they were subsequently observed.

average arrival date. Finally, an individual's sex did not explain its behavioural response type during the weather event and the null model was the most well-supported model ($w_i = 0.57$; Table S5, Supporting information).

SHORT-TERM CONSEQUENCES

Individuals remaining in the study area had higher estimated daily MMRs than individuals that reverse migrated ($\beta = 4.65$, $SE = 0.13$, $CI = -0.60, -0.09$; $w_i = 0.91$; Tables S5 and S6, Supporting information). On average, estimated daily MMR was 4.00 ± 0.47 W ($n = 24$) for individuals that left and 4.35 ± 0.43 W ($n = 24$) for individuals that stayed in the study area (Fig. 4). Male and female godwit winter basal metabolic rates (BMR) are 1.60 ± 0.04 and 2.15 ± 0.32 W, respectively (Gutiérrez *et al.* 2012). Per day, individuals thus saved 29.93 ± 19.92 kJ ($n = 24$) by reverse migrating – 8.8% of

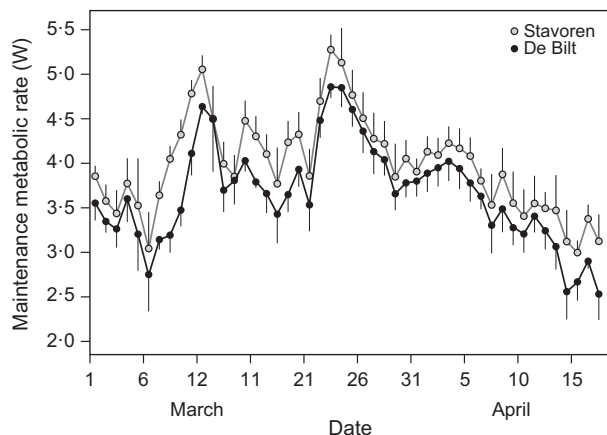


Fig. 4. Daily variation in estimated maintenance metabolic rate in watts for black-tailed godwits during March and April 2013 in Stavoren and De Bilt, the Netherlands. The black line represents Stavoren and conditions for godwits that remained in the study area; the grey line, De Bilt and conditions experienced by individual godwits making reverse migratory movements; error bars represent one standard deviation from the mean.

the estimated MMR for individuals in the study area and 16.3–21.9% of BMR. When combined with the cost of a round trip flight of 183.4 km (106 kJ each way), an individual needed to remain outside the study area 7 days to have saved energy by making the trip; the average duration of a reverse migration was 22 ± 12 days, meaning that such an individual could have saved ≥ 449 kJ during the course of its absence.

Foraging observations were made of 44 females in our Frisian study area, totalling 584 3-min foraging observations across 23 days. Females remaining in the study area increased their foraging rates during the periods with the lowest temperatures (Fig. 5, Tables S5 and S6). However, foraging efficiency – the number of prey items captured per probe – was negatively correlated with foraging rates ($\beta = -4.1 \times 10^{-5}$, $SE = 1.8 \times 10^{-5}$, $CI = 0.017, 0.023$; Tables S5 and S6), meaning that individuals had to increase their foraging rates by 12.5% to capture the same number of prey items on the coldest days. Nonetheless, females still captured 2.93 ± 0.74 ($n = 23$) more prey items per three-minute period on the coldest days. Besides temperature, no other variable or model received support (Table S5).

LONGER-TERM CONSEQUENCES

At the population level, the 2013 breeding season was delayed, but other reproductive parameters were comparable or above average (Table 1). The proportion of fields supporting territorial godwits was lower during the first three weeks of the season than in other years (Fig. 6; Tables S7 and S8, Supporting information) and mean lay dates were later (2013: $\bar{x} = 30$ April ± 9 days, $n = 814$) than in all but one other year (2007: $\bar{x} = 29$ Apr ± 11 days, $n = 343$; Tables 1 and S8). All other reproductive parameters, however, were either above average (e.g. daily

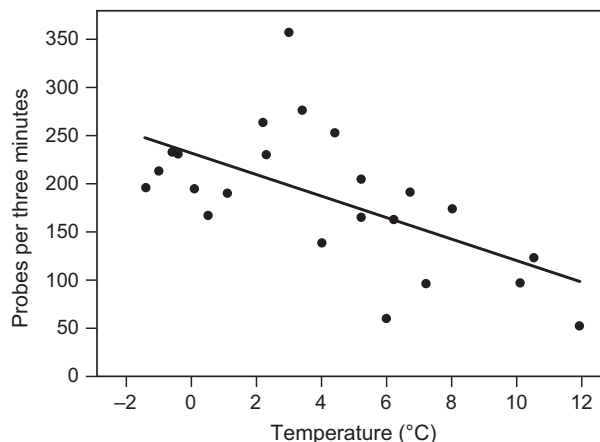


Fig. 5. Mean foraging rates of female black-tailed godwits during daylight hours ($n = 44$) in relation to daily minimum temperatures during March and April 2013 in Friesland, the Netherlands.

nest survival) or within the range of previously recorded values (e.g. return rate, peak number of parcels occupied, egg volume, clutch size and abandonment rate; Tables 1 and S8).

At the population level in 2014, fledging success was significantly lower than in 2013 (33.0 vs. 51.0%; Year: $\beta = -1.45$, $SE = 0.38$, $CI = -2.19, -0.71$), and nest abandonment rates were higher than in all other years (10.1%; $\bar{x} = 4.98 \pm 2.45$; Tables 1, S7 and S8). All other reproductive parameters, however, were either close to the mean or above average (Tables 1, S7 and S8).

At the individual level, no clear patterns linked behavioural response type to longer-term fitness consequences (Tables 2, S9 and S10). The null model was the most well-supported model in analyses related to breeding propensity ($w_i = 0.33$), clutch size ($w_i = 0.63$), egg volume ($w_i = 0.62$) and whether or not an individual's arrival date was delayed in 2014 ($w_i = 0.41$). Models containing the variable Year were the most well-supported models for nest initiation date ($w_i = 0.82$), daily nest survival ($w_i = 0.94$) and abandonment rate ($w_i = 0.59$; Table S10). Sex was the best predictor of return rate (Females: $\beta = -0.43$, $SE = 0.21$, $CI = -0.85, -0.02$; $w_i = 0.65$; Table S10), with only 71.8% of females returning ($n = 226$), as opposed to 79.5% of males ($n = 264$). This, however, was the typical pattern: across all years females were seen at a lower rate than males ($78.5 \pm 3.9\%$ vs. $84.5 \pm 4.7\%$; Females: $\beta = -0.58$, $SE = 0.15$, $CI = -0.88, -0.28$; Tables S6 and S7). Across all analyses, only one included behavioural response type in the most well-supported model (fledging success: Year + Response, $w_i = 0.59$; Table S9). This model identified the broods of those individuals that reverse migrated as having consistently higher rates of fledging success ($\beta = -25.56$, $SE = 11.31$, $CI = 3.39, 47.72$; Tables 2 and S10). Only one other behavioural response type variable was identified as being biologically relevant in any model: individuals that stayed in the study area throughout the weather event were consistently

Table 1. Interannual variation in reproductive parameters of black-tailed godwits breeding in Friesland, the Netherlands. Asterisks represent those parameters for which the most well-supported model identified 2013 or 2014 as being different from the majority of other years (Table S8). The study area was larger in 2013 and 2014, but research effort per unit remained consistent across years

Year	Number individuals resighted	Number of nests	Lay date	Clutch size (Eggs)	Egg volume (mL)	Hatching success	% Nests abandoned	Fledging success	% Individuals returning
2005–2012	250 ± 151	336 ± 147	26 April ± 11 days	3.7 ± 0.8	40.4 ± 2.9	49.3 (39.5 – 54.9)	5.0 ± 2.6	NA	81.1 ± 4.5
2013	591	814	30 April ± 9 days*	3.8 ± 0.8	40.3 ± 2.8	65.2 (61.2 – 69.0)*	4.9	51.0	80.0
2014	609	839	25 April ± 11 days*	3.8 ± 0.6*	40.6 ± 2.9*	50.4 (46.6 – 54.1)	10.1*	33.0*	76.1

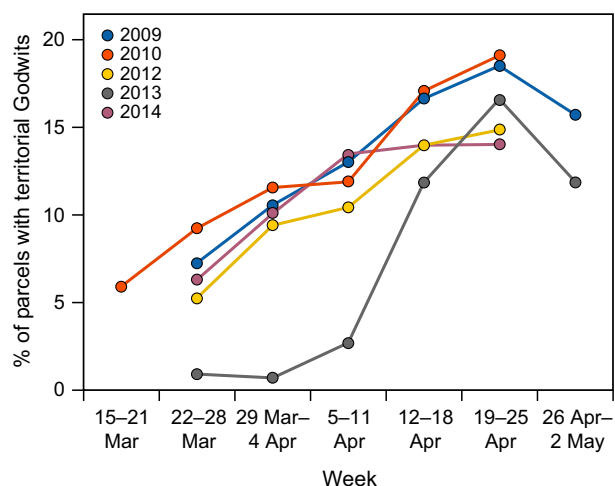


Fig. 6. Weekly estimates of the percentage of parcels ($n = 3257$) occupied by territorial black-tailed godwits in Friesland, the Netherlands 2009–2014.

more likely to breed than were individuals in other groups ($\beta = 0.79$, $SE = 0.39$, $CI = 0.02$, 1.55 ; Tables 2 and S10).

Discussion

We were able to follow individual godwits throughout the springs of 2013 – a period characterized by a late snow-storm, weeks of record low temperatures and months of below average temperatures – and 2014, making our study one of the first to document a population's response to a rare weather event at multiple spatial scales and across multiple years. We found that the event incurred real costs for godwits: individuals employed a suite of behavioural responses to cope with the circumstances, resulting in reverse migratory flights, increased foraging rates and delayed arrival on the breeding grounds. However, longer-term consequences were almost completely lacking and we found little evidence for carry-over effects impacting subsequent reproductive success or survival. Thus, while the weather event was extreme meteorologically, it was not extreme ecologically (Smith 2011). This suggests three key factors that are likely necessary for a population to withstand severe and extreme weather events or other short-term environmental stressors: (1)

continued access to food, (2) behavioural flexibility, and (3) time to dissipate the costs incurred by the event. Maintaining adequate habitat and healthy population sizes should therefore ensure that extreme events – that is those events in which both the environmental driver and the ecological response are extreme – remain truly rare (Malinowska *et al.* 2014).

Behavioural responses and their consequences

The weather event in 2013 disrupted godwit behaviour at all three spatial scales at which we tracked individuals. At the continental scale, satellite transmitter-carrying individuals migrated faster and stopped over fewer times in 2014 than 2013. This pattern was consistent with on-the-ground reports from across Western Europe in 2013, which described unusually large concentrations of godwits – nearly five times average peak counts in some cases – that remained stopped over for weeks in areas usually witnessing smaller concentrations of godwits staying for shorter periods of time (e.g. Devos, Desmet & Robbe 2014). Despite these delays and the widespread nature of the event, we did not detect instances of vagrancy outside of the normal godwit migratory corridor. Nor did godwits appear to delay departure from Iberian staging sites even after the onset of cold conditions in early March, meaning all migratory delays resulted from prolonged stopovers.

At the regional and local level, we detected two other behavioural responses. The majority of godwits arriving at breeding sites in south-west Friesland during the weather event subsequently migrated south again 90 to 250 km and remained outside of our study area for over three weeks, returning only after the cessation of the lowest temperatures. These birds largely congregated south of Lake IJsselmeer in the Netherlands, where the operative temperature – after accounting for wind speed – was on average 4 °C higher than in our study area. Those individuals remaining in the study area more than doubled their probing rates – enabling them to consume nearly three prey items per minute more than under warmer conditions – to offset the higher metabolic costs incurred by staying at more northerly latitudes. Additionally, we did document the starvation of one individual (with a

Table 2. Reproductive parameters of black-tailed godwits exhibiting different behavioural response strategies. Individuals were assigned a response type in 2013, but their behaviour and fitness tracked 2013–2014; thus, individuals were assigned to the same response type in both years. Asterisks represent parameters for which the most well-supported model identified one of the behavioural response types as being different from the others (Table S10)

Response type	Year	Number of individuals	Breeding propensity	Number of nests	Lay date	Clutch size (Eggs)	Egg volume (mL)	Hatching success \pm 95% confidence interval	Abandonment rate	Fledging success	Return rate	Proportion delayed
Stayed	2013	61	0.36*	22	30 April \pm 11 days	4.1 \pm 1.1	40.4 \pm 2.4	80.3 (46.3 – 93.9)	4.5	57.1 (n = 7)	83.6	NA
Reverse	2013	263	0.26	69	29 April \pm 8 days	3.8 \pm 0.5	40.4 \pm 2.8	82.7 (61.0 – 92.3)	0.0	66.7 (n = 9)*	74.9	NA
Delayed	2013	99	0.28	28	29 April \pm 7 days	3.8 \pm 0.6	40.8 \pm 2.8	90.6 (63.7 – 97.8)	3.6	20.0 (n = 5)	73.7	NA
Late	2013	66	0.20	13	1 May \pm 8 days	3.6 \pm 1.0	39.6 \pm 3.1	100.0	0.0	50.0 (n = 2)	75.8	NA
Stayed	2014	51	0.41*	21	26 April \pm 15 days	3.7 \pm 0.7	40.4 \pm 1.8	64.3 (30.3 – 85.1)	9.5	22.2 (n = 9)	NA	5.9
Reverse	2014	197	0.34	66	22 April \pm 11 days	3.8 \pm 0.4	40.8 \pm 2.9	50.7 (26.4 – 70.8)	7.5	58.3 (n = 12)*	NA	8.6
Delayed	2014	73	0.37	27	19 April \pm 11 days	4.0 \pm 0.0	39.7 \pm 3.0	47.9 (20.5 – 71.8)	0.0	0.0 (n = 5)	NA	11.0
Late	2014	50	0.34	17	21 April \pm 5 days	3.9 \pm 0.8	41.3 \pm 3.3	84.2 (30.0 – 97.8)	5.9	20.0 (n = 5)	NA	0.0

slightly aberrant bill) within our study area (Y. Galama, personal communication), suggesting that at least some individuals were unable to adequately respond to the weather event.

Although the costs were real, they had little effect on longer-term reproductive success and survival. In fact, across all groups, 2013 had higher rates of nest survival and fledging success than average and, while 2014 had reduced rates for both parameters, they were still above average for our long-term study and relative to other godwit demographic studies (Schekkerman, Teunissen & Oosterveld 2008). Taken together, the event ultimately appears to have had a *positive* effect on the population. This may have occurred because the colder conditions delayed local insect phenology, allowing godwits to properly align their reproductive efforts with peak food conditions for their chicks, something they are frequently unable to achieve (Schroeder *et al.* 2012; N. Senner, unpublished data). However, a potential negative consequence of the weather event may be an expected shift towards later lay dates for recruits hatched in 2013 (Gill *et al.* 2013), which could put the population at risk of an increased phenological mismatch in warm years (Kleijn *et al.* 2010; Schroeder *et al.* 2012).

Withstanding severe and extreme events

Given that other studies documenting the responses of populations to events similar to those detailed here have found evidence not only for carry-over effects (Studds & Marra 2011), but also significant mortality and even evolutionary change (Brown & Brown 1998), what could account for the lack of long-term repercussions in our study? Our results suggest that three factors may be key to enabling populations to withstand the effects of severe and extreme weather events:

- 1 Food availability.** Recent studies have found that starvation, and not the direct effects of environmental conditions themselves (i.e. hypothermia or heat stress), have been the cause of the fitness consequences incurred both during (Dietz & Piersma 2007; Deville *et al.* 2014; but see Boyle, Winkler & Guglielmo 2013) and after (Studds & Marra 2011) severe and extreme weather events. In contrast, our results suggest that even godwits remaining in our study area were able to forage successfully throughout the event. Nonetheless, a decrease in food availability may have been a driver of the observed reverse migratory movements.
- 2 Behavioural flexibility.** Godwits appeared to have significant behavioural flexibility enabling them to mitigate the costs of the weather event. For instance, a one-way flight of 92 km (i.e. the average reverse migration distance) costs a godwit 106 kJ; a less adept flier – such as greater flamingos, *Phoenicopterus roseus* (Deville *et al.* 2014) – might have incurred costs high enough to make even such a relatively short flight prohibitive. Later arriving godwits were also able to pause their migra-

tions and remain at stopover sites south of areas with the lowest temperatures, something that is impossible for some migratory species (Senner 2012). As such, godwits had a number of possible responses to the harsh conditions that were at least relatively successful at reducing the potential costs of the weather event. Those populations most severely impacted by severe and extreme events often lack even one such option, whether because of their inherent biology or because of anthropogenic factors (Newton 2006).

- 3 Stress dissipation.** Carry-over effects occur when trade-offs among life-history traits cause an individual to disproportionately allocate resources to one trait, resulting in suboptimal allocation of resources to life-history traits during a future life-history event (Harrison *et al.* 2011). Such processes occur more frequently when a bottleneck exists between the two life-history events, indicating selection is acting strongly and constraining resource allocation (Buehler & Piersma 2008). While the weather event in our study spanned spring migration and the pre-laying phase – two components of the annual cycle frequently suggested to be taxing – these periods likely do not represent bottlenecks for godwits. Instead, godwits have an unusually long interlude between arrival on the breeding grounds and nest initiation, meaning even under poor conditions godwits may have ample time to dissipate previously accrued stress and accumulate the resources necessary to successfully breed (Lourenço *et al.* 2011). In other species with a shorter pre-laying phase and narrower window for successful reproduction, dissipating the costs incurred by the weather event prior to the onset of laying and incubation likely would not have been possible and fitness consequences would be inevitable (Vézina *et al.* 2012).

Relationship between weather events and other short-term stressors

Although Smith (2011) defined extreme events in relation to weather-related events, the underlying physiological mechanisms with which organisms cope with acute stressors are the same no matter the cause (Wingfield, Kelly & Angelier 2011). Thus, populations that have access to food, behavioural flexibility and time to dissipate the costs induced by stressors should also be able to withstand the effects of other acute stressors, such as fire (Hossack & Piliiod 2011), disturbance (Goss-Custard *et al.* 2006) or the presence of predators (Cresswell 2008). Our study thus makes clear that not all stressors – even those that are seemingly extreme – will result in extreme ecological consequences. Extreme in the ecological sense requires that the strength of the response to an event be commensurate or even stronger than that of the event itself; such occurrences should therefore remain truly rare. Nonetheless, were godwits constrained with respect to any of the three factors we identified – because of other anthropogenic forces limiting

the availability of foraging habitat, for instance – the outcome of our study could have been different (Drake & Griffen 2013).

CONCLUSIONS

Fully capturing a population's response to stochastic weather events is difficult and rarely undertaken because of the rarity of the events and the need to study them in their full ecological context. This has led to ongoing uncertainty about how individuals and populations respond to such events and at what spatial and temporal scale those responses take place. This study helps to fill that void by combining detailed observations of the behaviour of individual migratory birds with movement and resighting data at local, regional and continental scales. Our findings indicate that not all extreme events have extreme ecological consequences and, therefore, that an in-depth understanding of populations and communities is necessary to pinpoint the expected repercussions of future increases in the incidence of severe and extreme events. Such knowledge can not only help forecast the impacts of global climate change, but also broaden our understanding of how organisms cope with stressful conditions and ultimately dissipate the costs of those stresses.

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Data accessibility

Field data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.91d70> (Senner *et al.* 2015a). Tracking data available from Movebank: <http://dx.doi.org/10.5441/001/1.m3b75054> (Senner *et al.* 2015b).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Highest-ranked models (with lowest AIC_c scores) in candidate sets for effects of year on migratory patterns of black-tailed godwits tracked with satellite transmitters from Extremadura, Spain in 2013 ($n = 14$) and 2014 ($n = 23$). Only models with model weight (w_i) > 0.10 are reported. K indicates the number of parameters in each model.

Table S2. Model-averaged coefficients for factors affecting migration patterns in northward migrating black-tailed godwits tracked with satellite transmitters from Extremadura, Spain in 2013 ($n = 14$) and 2014 ($n = 23$).

Table S3. Models (ranked by qAIC_c scores) in candidate set for effects of date on group resighting probability of individually colour-marked black-tailed godwits ($n = 324$) during March and April 2013 in southwest Friesland, The Netherlands.

Table S4. Model coefficients for factors affecting the resighting probability of individually colour-marked black-tailed godwits ($n = 324$) during March and April 2013 in southwest Friesland, The Netherlands.

Table S5. Highest-ranked models (with lowest AIC_c scores) in candidate sets for factors affecting the behavioral response type ($n = 490$), daily maintenance metabolic rate ($n = 24$), and foraging rate ($n = 23$) of black-tailed godwits during March and April 2013 in southwest Friesland, The Netherlands.

Table S6. Model-averaged coefficients for factors affecting the behavioral response type ($n = 490$), daily maintenance metabolic rate ($n = 24$), and foraging rate ($n = 23$) of black-tailed godwits during March and April 2013 in southwest Friesland, The Netherlands.

Table S7. Highest-ranked models (with lowest AIC_c scores) in candidate sets for effects of year on reproductive parameters and return rates of black-tailed godwits breeding in southwest Friesland 2005–2014.

Table S8. Model-averaged coefficients for factors affecting reproductive parameters and return rates of black-tailed godwits breeding in southwest Friesland, The Netherlands 2005 – 2014.

Table S9. Highest-ranked models (with lowest AIC_c scores) in candidate sets for effects of covariates on reproductive parameters and return rates of black-tailed godwits exhibiting different

responses to the climatic events of the spring of 2013. Only models with model weight (w_i) > 0.10 are reported.

Table S10. Model-averaged coefficients for factors affecting the reproductive parameters and return rates of black-tailed godwits exhibiting different behavioral responses to the climatic events of the spring of 2013.