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1 **Title page**

2

3 **Timing of spring departure of long distance migrants correlates with previous year conditions at**
4 **their breeding site**

5

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26

27

28 **Keywords (3 to 6)**

29 Circannual clock, migration timing, green-up date, phenology, Eurasian curlew, *Numenius arquata*

30

31 **Abstract**

32 Precise timing of the migration is crucial for animals targeting seasonal resources at locations
33 encountered across their annual cycle. Upon departure, long distance migrants need to anticipate
34 unknown environmental conditions at their arrival site, and they do so with their internal
35 annual clock. Here, we tested the hypothesis that long distance migrants synchronize their circannual
36 clock according to the phenology of their environment during the breeding season, and therefore
37 adjust their spring departure date according to the conditions encountered at their breeding site the
38 year before. To this end, we used tracking data of Eurasian curlews from different locations and
39 combined movement data with satellite-extracted green-up dates at their breeding site. Spring
40 departure date was better explained by green-up date of the previous year, while arrival date at the
41 breeding site was better explained by latitude and longitude of the breeding site, suggesting that
42 other factors impacted migration timing *en route*. On a broader temporal scale, our results suggest
43 that long distance migrants may be able to adjust their migration timing to advancing spring dates in
44 the context of climate change.

45

46 **Introduction**

47 Animal migration is an adaptation to seasonal variations in food resources and environmental
48 conditions [1]. The phenology of migration, and most importantly the timing of spring migration is
49 crucial to match the timing of reproduction with the peak of food resources and thereby maximize
50 breeding success [2,3]. When migrants leave their wintering grounds, they should ideally adjust their
51 departure with spring phenology at their breeding site. While for short-distance migrants local cues
52 at the wintering site can be good predictors of conditions at the breeding site [3], this is likely not the
53 case for long distance migrants [4]. Even large scale climatic indices such as the North Atlantic
54 Oscillation index (NAO) seems to be poor predictors of bird migration timing [4,5]. Therefore, for
55 long-distance migrants, environmental conditions at their breeding sites are likely to be unknown
56 when they depart. In this case, it has been proposed that the timing of spring departure is controlled
57 by an internal circannual clock, itself influenced by the photoperiod and other stimuli able to fine-
58 tune events year-round [2,3,6,7]. The underlying mechanisms synchronizing the circannual clock and
59 triggering departure of spring migration are still poorly understood [2,6].

60 To link the timing of migration with environmental conditions, one needs to assess spring onset over
61 a large geographical scale. At the scale of a continent, this can be done by monitoring the change in
62 colour of the vegetation with satellite imagery, to identify when budburst starts in deciduous forests
63 [8]. Even though green-up of the vegetation might not be the direct cue influencing the timing of

64 migrants, it gives a good proxy of spring phenology and is a particularly relevant approach when
65 studying breeding habitat of populations with a large breeding range [9–11].

66 Here, we propose to test whether long-distance migrants schedule their spring departure according
67 to the environmental conditions encountered the previous year at their breeding site, via the
68 synchronization of their circannual internal clock during the breeding season, rather than through
69 local cues at the wintering site. More specifically, we predict that the spring migration departure
70 date is correlated to the breeding site green-up date of the previous year, experienced by the bird,
71 rather than to the breeding site green-up date of the same year, not known at the time of departure.
72 We also predict that arrival dates at the breeding site are adjusted according to conditions
73 encountered *en route* [2,12,13].

74 We used a dataset of GPS tracked Eurasian curlews (*Numenius arquata arquata*, hereafter curlew)
75 nesting over a large area of Northeast Europe (including western Russia) and occupying contrasting
76 western European wintering grounds. Spring phenology at the breeding sites was assessed by the
77 green-up date of the vegetation measured by satellites.

78

79 **Material and methods**

80 *Tracking data*

81 A total of 35 complete spring migration tracks were obtained from 26 adult curlews in 2016 and
82 2017. Nine birds were tracked during two consecutive years. Deployments were made in three
83 countries, either during the non-breeding period (mid-July to mid-April; Germany, Wadden Sea coast,
84 n=7 and France, Pertuis Charentais, n=16) or during the breeding season (May; Estonia, n=3). Details
85 on the capture methods and deployment sites are given in supplementary material S1. GPS tags were
86 EOBS bird solar GPS-UHF tags (20g, e-obs GmbH, Gruenwald, Germany) in Estonia, Ecotone Sterna
87 GPS-UHF (35x16x10 mm, 7.5g) in France and Ecotone Skua GPS-UHF-GSM (58x27x18mm, 17g) in
88 Germany (Ecotone Telemetry, Gdynia, Poland). GPS tags recorded fixes every 5-60 minutes.

89 To extract nest positions from the GPS tracks, we isolated the breeding period and counted the
90 number of positions within each cell of a grid (0.0001°x 0.0001°) covering the range of longitudes and
91 latitudes visited by each individual during the breeding period. The position of the nest was defined
92 as the center of the cell with most counts.

93 Migration dates (day of year) were obtained by visual examination of the tracks on QGIS [14].

94 Departure and arrival were defined as the first and last location on a migration bout (highly

95 unidirectional flight, high speed). When birds showed a prospecting behaviour upon arrival at their
96 breeding ground, the arrival date was determined as the first stop within a 10 km radius around the
97 nest site.

98 *Green-up date of the vegetation as an index of spring phenology*

99 Satellite remote sensing has often been used to study leaf phenology of various ecosystem types.
100 We used the method by Delbart et al. [8] which determines the spring date when the ecosystem
101 greens-up (hereafter green-up date). This method uses a combination of near and short-wave
102 infrared spectral bands, instead of the “classic” vegetation spectral index based on the red and near-
103 infrared bands; this avoids disturbance of the radiometric signal by snowmelt which affects other
104 algorithms [15,16]. Over boreal forests, the green-up date is closely related to the observed leaf
105 budburst date of deciduous trees with an 8-day root-mean-square difference (RMSD) with budburst
106 observations [8,17]. This RMSD arises from the remote sensing data pre-processing that retains only
107 the cloud-free observations and reduces the observation frequency, and from the phenological
108 variability within the pixel that the method cannot catch. Nevertheless, this method allows
109 monitoring interannual variations in phenology [17–19]. The remote sensing method is here applied
110 to PROBA-V data from 2014 to 2017, and our study area is located where the method’s reliability is
111 the highest [8,16,18]. Details are presented in supplementary material S2.

112 For each nest site, green-up date was calculated for a 10-km buffer around the nest. Curlews are
113 extremely faithful to their breeding site [20], and breed within <5km of their previous nest site
114 (Bocher, unpublished data). Thus, we assumed that they were breeding at the same location the
115 previous year, which was the case for all curlews tracked for more than one year in our dataset. One
116 bird captured in France bred in Germany in an area located in the temperate zone, whereas the
117 remote sensing method has been designed for continental and polar bioclimatic zones [21].
118 Nevertheless, as it was not an outlier in our data it was kept in the analyses. We tested whether
119 green-up dates differed between two consecutive years, using a Wilcoxon signed-rank test (Fig. S1).

120 *Statistical analyses*

121 Statistical analyses were performed under R 4.0.3 [22]. We used linear mixed effect models (nlme
122 package [23]) to take into account the fact that some birds were sampled twice and that we sampled
123 at three different locations, following methods described in Zuur et al. [24]. We used a model
124 selection approach based on Akaike Information Criterion (AIC) [25] and compared seven models to
125 identify which variables best explain the migration dates of curlews (Table 1). We modelled
126 departure or arrival date of the spring migration as a function of green-up date of the current year
127 (model 1), the previous year (model 2) or two years prior (model 3). Green-up dates of successive

128 years were correlated and were therefore not included in the same model. The green-up date two
129 years prior was included as a negative control, i.e. we did not expect it to be a good predictor of
130 timing of migration according to our hypothesis. A fixed effect “year” was included because the
131 timing of spring can differ between years over the whole study area. We also modelled departure
132 and arrival dates as a function of the mean green-up date for the study period (2014-2017, model 4),
133 and as a function of the nest latitude and longitude (models 5-7) to test whether curlews rather leave
134 according to the average conditions they experienced or based on the location of their nest. The
135 random term contained “individual” nested in the country of capture (France, Germany or Estonia) to
136 take into account sampling groups and repeated measurements per individual. Models were
137 compared using the AIC corrected for small sample sizes (AICc) and all models with a $\Delta AICc$ lower
138 than 2 were considered equally good [26]. We graphically checked the selected models for
139 homogeneity, independence and normality of the residuals [24]. A repeatability index (intraclass
140 correlation coefficient) was calculated for individuals tracked two successive years, using the R
141 package ICC [27].

142

143 Results

144 Tracked curlews bred over a large part of the subspecies breeding range [20]: from 9.35°E to 52.24°E
145 and from 52.75°N to 64.54°N (Fig. 1). Mean migration distance was 2453 ± 754 (sd) km
146 (supplementary table S1). Median departure date was April 10th (range March 16th – May 4th).
147 Median arrival date was April 23rd (range March 17th – May 14th). Departure and arrival dates were
148 correlated to the green-up date of the vegetation at the breeding site (Fig. 2, Table 1). Individual
149 spring departure date from the wintering site was best explained by the model containing green-up
150 date of the previous summer and year as fixed effects (Table 1a, Fig. 2). Arrival date at the breeding
151 site was best explained by the model containing longitude and latitude of the nest (Table 1b). The
152 green-up dates at nest sites were significantly different between two successive years with on
153 average earlier green-up dates in 2016 than 2015 and 2017 (Fig. S1; Wilcoxon signed-rank test: 2016:
154 p-value = 0.04, effect size $r = 0.50$, $n = 17$; 2017: p-value <0.001, effect size $r = 0.87$, $n = 18$). For nine
155 birds tracked during two consecutive spring migrations, repeatability was 0.88 (95% CI: 0.60-0.97) for
156 the departure date, and 0.91 (95% CI: 0.68-0.98) for the arrival date.

157

158 Discussion

159 Using a unique dataset of long-distance migrant tracks gathered by three European research teams
160 over two years with contrasting spring phenology, we demonstrate that the onset of spring migration
161 in Eurasian curlews is correlated with environmental conditions at their breeding site (spring
162 phenology) encountered the previous year. Our results thus suggest that curlews might fine-tune
163 their annual endogenous clock during the breeding season for the coming year and use this clock to
164 depart on time for the next spring migration. Arrival at breeding sites was however better explained
165 by longitude and latitude of the nest, suggesting that other environmental factors impact migration
166 timing *en route* [12].

167 From an evolutionary perspective, synchronizing the circannual clock and subsequent annual
168 movements during the breeding season appears to be the most relevant strategy, as this period is
169 critical for individual fitness, especially for migrants breeding in highly seasonal environments where
170 the optimal window to reproduce is short [28]. By doing so, long-distance migrants use their own
171 experience to schedule departure at a time when they cannot rely on local cues at their wintering
172 site to anticipate conditions at their breeding ground. Since most bird migrants pairs do not migrate
173 together nor overwinter at the same place [3], setting the circannual clock and the onset of spring
174 migration according to the previous breeding season allows to ensure synchrony among the pair,
175 which is known to reduce the risk of divorces and improve the pair's reproductive success [29,30]. An
176 alternative hypothesis could be that curlews may gain experience year after year and adjust their
177 migratory behavior based on more than one breeding event. This hypothesis was not supported by
178 our results as the average green-up date did not perform better to explain the departure dates. A
179 longer dataset would be required to obtain across lifetime green-up dates and further investigate
180 this possibility.

181 Among all yearly events in a migratory bird life cycle, the onset of spring migration appears to be the
182 least variable, both in natural conditions [31,32] and for captive birds under constant conditions
183 [2,33]. This most likely reflects the constrained time window to reproduce in seasonal environments
184 [28]. Yet other parameters may also influence this timing, such as climatic conditions, winter habitat
185 quality, social interactions or age [34–37], and as proposed here previous breeding conditions.
186 Similarly, the timing of migration can be adjusted after the departure, along the way and according
187 to local environmental cues that become more and more informative the closer the bird gets to the
188 breeding grounds [11–13,32]. The differences in models selected for the departure and arrival dates
189 in our study suggest that some of the above mentioned environmental factors influence migration
190 timing *en route*. Yearly events are therefore dependent on the circannual clock, but constantly fine-
191 tuned by environmental factors [2,3].

192 While we used green-up date of the vegetation as an indicator of spring phenology at the curlew's
193 breeding site, it is probably a proxy only for other tightly linked cues [9] which directly influence their
194 breeding success and which can be used by birds to synchronize their cycle. For curlews, it might be
195 insect peaks and access to other invertebrate prey, essential to ensure chick provisioning and survival
196 [38] or vegetation height, important for incubating parents and chicks to hide from predators in such
197 ground nesting meadow birds [39].

198 In the context of global warming, changes in migration dates have been observed at the population
199 level [10,40,41]. In contrast, at the individual level, most studies tracking migratory birds across
200 several years found a high individual consistency in the timing of migration (e.g. [5,31,42–46], but see
201 [47]), including our study where the repeatability of migration dates was similar to previous findings
202 from other migratory birds [31,43,46]. Previous studies conclude that there is a low phenotypic
203 plasticity in the timing of migration, and eventually a mismatch with food resources leading to
204 negative consequences on fitness [48]. Individual consistency in the timing of migration in these
205 studies could also be explained by the repeatability of spring timing of the environment from year to
206 year, and may not necessarily imply a low phenotypic plasticity. As shown by the correlation we
207 found between spring departure date and green-up date of the previous year at the breeding site,
208 we propose that there might be some plasticity in the timing of migration, which allows a synchrony
209 of the breeding activity with phenological changes of the environment. Further investigations are
210 needed to test this hypothesis on different species and with longer repeated measurements from the
211 same individuals in order to better evaluate phenotypic plasticity and possible adjustments to
212 ongoing global changes.

213

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223

224 **Data accessibility**

225 The dataset supporting this article [49] is deposited at <https://doi.org/10.5061/dryad.8sf7m0cp6>.

226

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228

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361 Table 1: summary of statistical models. GU_n = green-up date of the same year than the migration.
 362 GU_{n-1} = green-up date of the previous year. GU_{n-2} = green-up date two years prior (used as a control).
 363 AvgGU = average green-up date for the period 2014-2017. Longitude and latitude of the breeding
 364 site. Models with the smallest AICc are represented in bold and their estimates are given below.

(a) departure date

Model selection

N°	Model	DF	AICc	Δ AICc	
1.0	Intercept		4	254.12	30.54
1.1	GU_n +Year		6	226.66	3.08
1.2	GU_{n-1}+Year		6	223.58	0.00
1.3	GU_{n-2} +Year		6	235.81	12.23
1.4	AvgGU		5	233.26	9.68
1.5	Latitude		5	230.38	6.80
1.6	Longitude		5	245.34	21.76
1.7	Latitude + Longitude		6	230.21	6.63

Parameter estimation

Model		Estimate	SE	t-value	p-value
N°	Parameter				
1.2	Intercept	34.01	10.71	3.18	0.0042
1.2	GU_{n-1}	0.56	0.08	6.75	0.0003
1.2	Year 2017	-2.57	1.31	-1.96	0.0909

(b) arrival date

Model selection

N°	Model	DF	AICc	Δ AICc	
2.0	Intercept		4	275.19	47.4309
2.1	GU_n +Year		6	243.61	15.8473
2.2	GU_{n-1} +Year		6	244.89	17.1270
2.3	GU_{n-2} +Year		6	256.30	28.5429
2.4	AvgGU		5	235.51	7.7500
2.5	Latitude		5	233.96	6.2000
2.6	Longitude		5	261.19	33.4300
2.7	Latitude + Longitude		6	227.76	0.0000

Parameter estimation

Model		Estimate	SE	t-value	p-value
N°	Parameter				
2.7	Intercept	-86.50	19.15	-4.52	0.0002
2.7	Longitude	0.42	0.13	3.15	0.0162
2.7	Latitude	3.04	0.35	8.68	0.0001

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367 Figure legends

368 Figure 1: Nest sites of curlews, and mean green-up dates for years 2015-2017. Dates are given as day
369 of the year.

370

371 Figure 2: Relationship between spring migration date and green-up date of the previous year.

372 Orange: year 2016, blue: year 2017. Dots represent data. Lines represent the fitted values and 95%
373 confidence interval of model 1.2 (table 1). All date units are day of the year.

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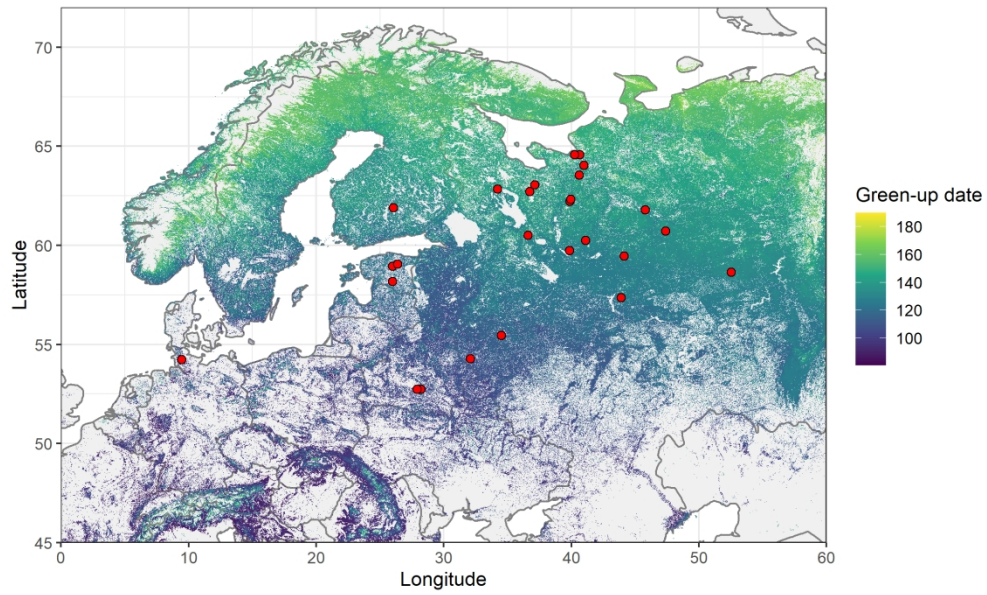


Figure 1: Nest sites of curlews, and mean green-up dates for years 2015-2017. Dates are given as day of the year.

199x119mm (300 x 300 DPI)

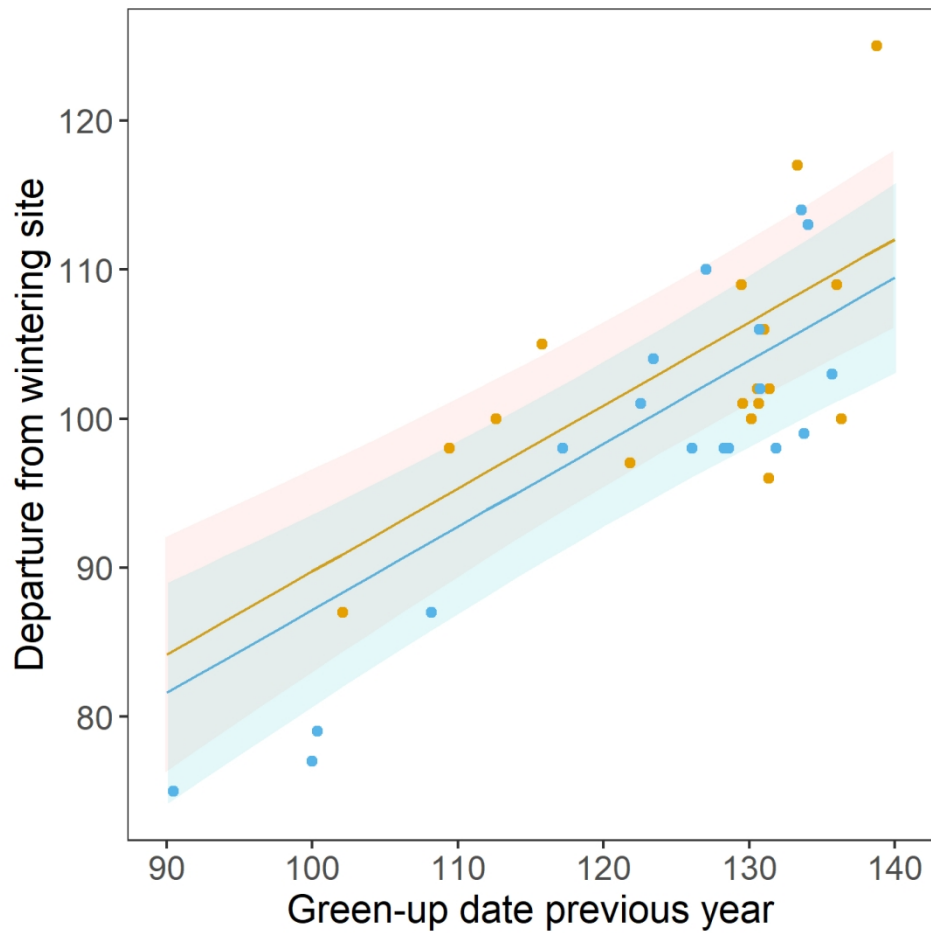


Figure 2: Relationship between spring migration date and green-up date of the previous year. Orange: year 2016, blue: year 2017. Dots represent data. Lines represent the fitted values and 95% confidence interval of model 1.2 (table 1). All date units are day of the year.

127x127mm (300 x 300 DPI)