Effect of weather conditions on the spring migration of Eurasian Woodcock and consequences for breeding

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Migration is a critical period of time with fitness consequences for birds. The development of tracking technologies now allows researchers to examine how different aspects of bird migration affect population dynamics. Weather conditions experienced during migration are expected to influence movements and, subsequently, the timing of arrival and the energetic costs involved. We analysed satellite-tracking data from 68 Eurasian Woodcock Scolopax rusticola fitted with Argos satellite tags in the British Isles and France (2012–17). First, we evaluated the effect of weather conditions (temperature, humidity, wind speed and direction, atmospheric stability and visibility) on migration movements of individuals. Then we investigated the consequences for breeding success (age ratio) and brood precocity (early-brood ratio) population-level indices while accounting for climatic variables on the breeding grounds. Air temperature, wind and relative humidity were the main variables related to migration movements, with high temperatures and northward winds greatly increasing the probability of onward flights, whereas a trend towards greater humidity over 4 days decreased the probability of movement. Breeding success was mostly affected by climatic variables on the breeding grounds. The proportion of juveniles in autumn was negatively correlated with temperature in May, but positively correlated with precipitation in June and July. Brood precocity was poorly explained by the covariates used in this study. Our data for the Eurasian Woodcock indicate that, although weather conditions during spring migration affect migration movements, they do not have a major influence on subsequent breeding success.

Keywords: age ratio, Argos transmitter, breeding ground conditions, carry-over effects, early-brood ratio.

The most common way for birds to cope with seasonal changes in weather and feeding conditions is to make flights between separate wintering and breeding grounds, a mechanism which has a strong genetic basis (Berthold et al. 1990, Berthold & Helbig 1992, Pulido et al. 1996, Pulido 2007, Liedvogel et al. 2011, Liedvogel & Lundberg 2014). The expression of this behaviour in a population is related to the fitness of migrating individuals vs. resident ones, e.g. by breeding and/or wintering in habitat with higher resources, lower predation risk and/or less competition (Alerstam et al. 2003, McKinnon et al. 2010). Undertaking migration, however, carries potential costs. It encompasses an important part of the annual cycle (up to 40–60% for some long-distance migrants, Newton 2011) and comprises a period during which birds cross unknown areas with uncertain food resources, weather conditions and predation risk. Conditions experienced during migration may thus have major effects on the timing and energetic costs of the journey (Jenni & Schaub 2003), as well as on individual survival (Klaassen...
et al. 2014). For instance, food abundance and availability at stopover sites are known to be important variables influencing the duration of stopovers for refuelling (Newton 2006). Moreover, the weather conditions such as wind strength and direction (Liechti 2006, Shamoun-Baranes et al. 2017) experienced during the trip strongly influence migration progress, depending on the flight strategy of the species, i.e. soaring or flapping flight, fuel deposit capacity and altitude of flight (Alerstam 2011).

Pre-breeding migration has profound consequences for the breeding season. Indeed, it sets important characteristics for breeding, such as the date of arrival at the breeding ground and body condition on arrival. The latter determines the capacity of the bird to invest energy directly in breeding activity (Sandberg & Moore 1996) and the former constrains the timing of breeding, e.g. breeding success may depend on the relationship between hatching date and seasonal availability of food for chicks (Both et al. 2005, Möller et al. 2008, Saino et al. 2011). The energetic cost of migration is especially important for species using stored resources for breeding, i.e. capital breeders (Stephens et al. 2009), but the timing of migration has consequences for breeding whatever the breeding strategies of the species (Both & Visser 2001, Newton 2006).

The study of bird migration has been revolutionised by the miniaturization of geolocation technologies, which now enable the tracking of most birds throughout their travels. The large amount of geolocation data recorded has revealed unexpected migration routes and behaviours (Burger & Shaffer 2008, Klaassen et al. 2014, Weimerskirch et al. 2015). This technology also offers new opportunities to study the mechanisms and factors driving migration strategy at the individual level. One of the main challenges lies in linking these geolocation data to relevant information on the factors expected to influence bird movements at relevant spatial and temporal scales (e.g. meteorology, Shamoun-Baranes et al. 2010). Remote sensing data appear to be the best solution, because it is almost impossible to realize field surveys at each bird position (Gordo 2007). Worldwide data are now easily available from public datasets, e.g. land cover classification, vegetation indices and climate datasets, which offer valuable information on parameters affecting bird migration.

This study focuses on the effect of weather conditions on the pre-breeding migration of a cryptic bird, the Eurasian Woodcock Scolopax rusticola (hereafter Woodcock). It is a widespread species living in woodland habitats. It has a broad diet, composed mainly of lumbricids, myriapoda and arthropods. The spring migration of the Woodcock alternates between flights of several hundred kilometres at night and stopovers for one or several days (https://Woodcockwatch.com; http://www.becassesmigration.fr; Crespo et al. 2016). Food abundance and availability play an important role in habitat selection during winter (Duriez et al. 2005) but are not expected to influence migration movements because most of the habitats crossed during migration are suitable for Woodcock (Crespo et al. 2016). However, weather conditions are expected to have a large influence on stopover duration during Woodcock migration and, consequently, on the duration of the complete spring migration.

To test this, we linked satellite tracking data from 68 individuals with remote sensing datasets available daily at a global scale. The effect of 14 climatic variables expected to affect bird migration, related to wind, temperature, visibility, humidity and atmospheric conditions (Richardson 1990a, Shamoun-Baranes et al. 2017), and when relevant their trends over a few days, were first tested to explain the migration movements of Woodcock at the individual level. We then investigated the consequences of weather conditions experienced during migration on the breeding success (proportion of juveniles) and brood precocity (proportion of juveniles having completed their post-juvenile moult) during the subsequent breeding season at the population level. However, because the energetic needs of breeding are thought to be gained mainly from local resources, especially for an income breeder such as Woodcock (see Stephens et al. 2009), the timing and success of breeding will also depend on climatic variables on the breeding grounds (Guzmán & Arroyo 2015). Temperature and precipitation on the breeding grounds were thus calculated and included in the analyses. We discuss the implications of our findings for Woodcock population dynamics and, more generally, for our understanding of carry-over effects of spring migration conditions on the reproductive success of migratory birds.
METHODS

Migration movements

From 2012 to 2017, 87 Woodcock were fitted with Argos satellite tags (solar PPT Microwave Telemetry, Inc., Columbia, MD, USA; 9.5 g) in February–March in Western Europe (63 in the British Isles in 2012–17 and 24 in France in 2015–16). Tags were attached to the birds using a leg-loop harness (Rappole & Tipton 1991) composed of 1.6-mm-diameter, UV-resistant, marine-grade rubber cord (EPDM cord; Polymax Ltd, Bordon, UK) passed through biomedical tubing (Silastic tubing; Cole Palmer, St Neots, UK). The tag schedule alternated between a 10-h ON period (Argos messages transmitted every 60 s) and a 48-h OFF period (no messages transmitted). Some of the 87 tags failed prematurely and some others failed to transmit any signal during spring migration. Moreover, several Woodcock were resident in the UK (no migration data) and some others died (hunted or unknown causes). Consequently, only 68 tags from the 87 used provided meaningful data for studying spring migration.

The spring tracking data were converted to a binary variable indicating whether the bird had continued its migration (1) or not (0) between two ON periods (first 10 h ON + 48 h OFF + next 10 h ON, i.e. 68 h elapsed time). A buffer of 50 km was defined to assess whether the distance travelled between the two ON periods corresponded to local movement or a migration flight. The threshold of 50 km was chosen according to the home-range of Woodcock during the breeding period, when movements were typically < 50 km (mean ± sd = 14 ± 23 km, n = 12). Such binary data thus described the probability of migration movement where at least two accurate locations were transmitted during a 68-h period. In total, 729 spring locations from 68 individuals were used (Fig. 1). Spring migration movements in more than 1 year were recorded for 31 individuals, with some birds yielding data for up to five consecutive years.

Weather variables were extracted from the NCEP Reanalysis (Kalnay et al. 1996) 2.5° × 2.5° gridded data provided by the NOAA/OAR/ESRL PSD (Boulder, CO, USA) website (http://www.esrl.noaa.gov/psd/). Fourteen weather variables related to wind, temperature, humidity, visibility and atmospheric conditions (see Table S1 in Appendix S1 for details) and, when relevant, their trends over 4 days were extracted. The accuracy of these variables was not available, which may have introduced additional uncertainty into the analysis (see Baker et al. 2017). All weather variables were available four times daily, but only information at 18 h (UTC) was extracted because Woodcock migration movements started at dusk. Moreover, all altitude-dependent weather variables were extracted near the ground surface because GPS loggers fitted on Woodcocks showed that they mainly migrate at low altitude (A. Hoodless unpubl. data). Weather variables were averaged over 3 days (time t, t + 1 and t + 2) to fit the tracking data time resolution (time t corresponded to the first 10-h ON period; time t + 1 and t + 2 to the 48-h OFF period) and their trends were assessed over 4 days (adding the previous day, t – 1).

Age and early-brood ratios

The effect of weather conditions experienced during spring migration on subsequent breeding ideally would be investigated at the individual level. However, tracking data did not provide reliable information about breeding success. Frequent movements of females during the breeding period indicated incomplete incubation, but this was insufficient to assess breeding success confidently. However, the proportion of juveniles (hereafter age ratio) and the proportion of juveniles having finished their post-fledging moult before migration (hereafter early-brood ratio) were available each year from French and Russian monitoring schemes.

Hunting of Woodcock wintering in Western Europe is popular, especially on the wintering grounds and during autumn migration. In France, a non-profit organization of Woodcock hunters (Club National des Bécassiers) collected wings of hunted Woodcock in order to determine the age and progress of moult (8000–10 000 wings collected each year). At the same time, a ringing programme was managed by a governmental organization (Office National de la Chasse et de la Faune Sauvage – ONCFS) and hunter organizations (Fédération Nationale des Chasseurs – FNC, Fédérations Départementales des Chasseurs – FDC). Thousands of birds (5000–7000) were ringed in France each year through this programme and the age and moult of individuals were assessed. Tens to a few hundred Woodcock were also caught in
autumn near their breeding grounds in Central Russia, thanks to a partnership between ONCFS and a Russian organization (BirdsRussia).

Age (juvenile or adult) can be assessed easily for Eurasian Woodcock using plumage characteristics (Clausager 1973, Ferrand & Gossmann 2009), and age ratio (proportion of juveniles) provided an index of breeding success at the population level. The age ratio of birds caught in Central Russia in early autumn was especially valuable because it gave a measure of breeding success at the start of autumn migration. However, the number of individuals caught was low in comparison with the thousands of birds collected each year in France. The moult stage of juveniles in autumn/winter gave important information on their hatching date because early-hatched juveniles (early broods) moulted all their secondary coverts, whereas late-hatched juveniles (late broods) showed some juvenile coverts (autumn migration stops moult of the wing feathers, Ferrand & Gossmann 2009). The proportion of early-brood juveniles therefore provided information on breeding phenology and its possible consequences for breeding success, e.g. higher mortality rate in chicks reared later.

To link such population-level indices with spring migration weather, the tracking data locations and dates were used as a sample to represent Woodcock flyway movements. Important weather variables found to affect migration movement were extracted from 1996 to 2017 for each location and date. As in the migration movement analysis, weather variables were averaged over 3 days (time $t$, $t + 1$ and $t + 2$) and their trends assessed over 4 days (adding $t - 1$). All values were then averaged yearly, which resulted in a unique set of weather conditions each year and enabled a correlative analysis with the breeding indices. We considered three scenarios of change in migration phenology from 1996 to 2017: (1) no change; (2) a linear shift of $\frac{1}{4}$ day per year (based on mean spring passage at Helgoland; Hüppop & Hüppop 2003); and (3) a non-linear shift driven by spring precocity. Scenario (2) was evaluated by retrospectively shifting migration dates by 1 day every 4 years because weather conditions were only extracted in the evening. Scenario (3) was achieved using air temperature data extracted for scenario (1) to give an index of rise in spring temperature at the flyway scale. An annual delay or advancement in spring temperatures was then calculated. This variable was scaled, as the overall trend from 1996 to 2017 corresponded to a general shift of $\frac{1}{4}$ day per year, as in scenario (2). The difference in temperature values was then converted into a number of days, which allowed a non-linear shift of dates to be considered.

Age and early-brood ratios were also expected to be influenced by weather on the breeding grounds. If so, failing to account for these variables may lead to fallacious results due to...
spurious correlations between weather during spring migration and the breeding period. Monthly mean temperature and precipitation in May, June and July from 1996 to 2017 were therefore extracted from known breeding locations of 63 tracked Woodcocks. Total precipitation from January to April was extracted as an index of pre-breeding soil–water conditions each year.

Statistical analyses

The effect of weather conditions on spring migration movements was examined using generalized linear mixed models, with a binomial error term and a logit link function. Weather variables were added as fixed effects and the individual bird was specified as a random effect. Candidate covariates (fixed effects) were chosen according to prior knowledge or their expected effect on migration movements. It was not possible to consider all subsets of these candidate covariates ($2^k$ possibilities with linear effects). Covariate selection was thus done in several steps starting from a model including only temperature and wind effects (strong support from prior knowledge). In total, about 150 subsets of covariates were considered (weather conditions and individual-based variables, e.g. age and breeding location) while avoiding collinearity between covariates (cross correlation $< 0.7$, see Dormann et al. 2013). All subsets of covariates were then classified according to Akaïke’s information criterion (AIC) and we retained the best model and alternative models having $\Delta$AIC $< 2$, i.e. those having ‘substantial support’ according to Burnham and Anderson (2002). Row coefficients of the models and their uncertainty are provided in Appendix S2 (see Table S2) and averaged parameters were calculated from this subset of models (Symonds & Moussalli 2011). Model selection was performed on a subsample of 668 observations for which there were no missing values for any of the covariates. However, coefficients were estimated from the maximum number of observations with no missing value in the set of covariates considered (from 668 to 729 depending on the covariates considered). Model residuals were checked for spatial correlation.

The effects of climatic variables extracted on the breeding grounds, and the weather conditions during migration on age and early-brood ratios, were investigated using linear models with normal errors. Model residuals were visually checked for normality. A linear model accounted for overdispersion due to the independent variance parameter $\sigma$ of the error term, whereas the use of a binomial model would imply that variance was a function of the mean, which ignores overdispersion. An alternative would be to use quasi-binomial models, but AIC could not be strictly evaluated with such an approach. Note that the results remained equivalent using either quasi-binomial or linear models. The source of data (birds ringed in Russia, ringed in France or hunted in France) was used as a factor to account for the differences between these sources, ensuring that covariates explained relative changes. Results remained unchanged whether data source was considered as a random or a fixed effect. Parameters were estimated by weighted least squares to account for the differences in the number of individuals $n_i$ used to calculate age and early-brood ratios.

Candidate climatic variables were those selected in the migration movement analysis (eight variables from the best model selected) and conditions at the breeding grounds (seven variables, see above). These covariates could not all be considered in the same model because the number of covariates considered was high relative to the number of observations, and because of collinearity between some of them. The analysis was thus carried out considering two main potential drivers of variation in observed index values: (1) the climatic variables extracted on the breeding grounds and (2) the weather conditions experienced during migration. The second potential driver of variation was investigated by testing the three scenarios detailed above on the changes in migration phenology since 1996, i.e. (scenario 1) no change in migration dates, (scenario 2) a shift of $\frac{1}{4}$ day per year and (scenario 3) an annual change in migration dates depending on air temperature. Covariate selection was done independently for each of these four sets of covariates (see Tables S3 and S7, in Appendices S3 and S4, respectively). Model selection was carried out using a corrected AIC (AICc) with $n = 23$ (number of studied years). AICc was compared between the different scenarios, which allowed assessment of the main cause of variation in age ratio and early-brood ratio.
RESULTS

Migration movements

Variable selection based on AIC resulted in retention of 15 models with $\Delta$AIC $< 2$. The models had from 10 to 15 parameters (Table 1, Appendix S2). Air surface temperature, winds (especially northward wind), atmospheric stability and relative humidity trend were the main weather variables associated with migration movements (Table 1, Fig. 2). These variables were present in all of the 15 competing models, and their coefficients were very similar across them (see Appendix S2). Air pressure and relative humidity were selected in most of the alternative models, but the estimated coefficients showed high uncertainties. Neither cloud cover nor cloud ceiling height (visibility) were selected in the models. The same was true for vertical wind speed and soil wetness. Precipitation rate had a skewed distribution, which prevented a good evaluation of its effect on migration movements.

Migration movements more frequently occurred in the presence of positive air surface temperatures (> 3 °C), stable atmospheric conditions (positive best four-layer lifted index) and favourable winds (especially northward winds, Fig. 2). A quadratic effect was fitted to atmospheric conditions, such that the highest values resulted in a decrease in movement probability, but the number of observations with such extreme conditions was small and, hence, the uncertainty was high. Conversely, migration movements occurred less frequently in the presence of a slightly decreasing or stable relative humidity trend. Uncertainty was very high for conditions with a strongly decreasing relative humidity trend (Fig. 2). Bird breeding origin (longitude and/or latitude of breeding area, linear migration distance; Table 1) also showed weak positive correlations with probability of migration movement. Longitude of the breeding area (Fig. 2) was the variable which best highlighted this correlation, with reduced uncertainty in most of the models considered (Table 1, Appendix S2). Selected interactions (lifted index $\times$ air pressure trend and eastward $\times$ northward wind) enhanced AIC values, but coefficient estimates showed high uncertainty.

Age and early-brood ratios

The proportion of young among late autumn and winter birds collected in France was lower than that of Russian birds caught in early autumn. Moreover, age ratio differed between ringed and hunted individuals in France, but both showed synchrony over time (Fig. 3a, $r = 0.79$, $n = 21$ years). All the models considered accounted for these differences through inclusion of the factor ‘type of data’. Variable selection showed that the lowest AIC was achieved by a model accounting for the climatic variables during the breeding period (Table 2, Table S3 in Appendix S3). The alternative best model, accounting only for weather conditions during spring migration, was that of the non-shifted migration hypothesis, but it performed very poorly ($\Delta$AIC > 30, Table S4). The most important variables correlating with age ratio

Table 1. Averaged parameters from the best set of models (15 models with $\Delta$AIC $< 2$, see Table S2 in Appendix S2) on the probability of migration movement.

<table>
<thead>
<tr>
<th>Covariates (scaled)</th>
<th>Averaged coefficients</th>
<th>Averaged standard errors</th>
<th>t-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.60</td>
<td>0.15</td>
<td>3.95</td>
</tr>
<tr>
<td>Longitude of breeding area</td>
<td>0.23</td>
<td>0.11</td>
<td>2.03</td>
</tr>
<tr>
<td>Air temperature</td>
<td>0.74</td>
<td>0.13</td>
<td>5.73</td>
</tr>
<tr>
<td>Eastward wind</td>
<td>0.15</td>
<td>0.09</td>
<td>1.66</td>
</tr>
<tr>
<td>Northward wind</td>
<td>0.50</td>
<td>0.10</td>
<td>4.90</td>
</tr>
<tr>
<td>Air pressure</td>
<td>0.15</td>
<td>0.10</td>
<td>1.46</td>
</tr>
<tr>
<td>Air pressure trend</td>
<td>0.14</td>
<td>0.10</td>
<td>1.40</td>
</tr>
<tr>
<td>Best four-layer lifted index</td>
<td>0.23</td>
<td>0.12</td>
<td>1.90</td>
</tr>
<tr>
<td>(Best four-layer lifted index)$^2$</td>
<td>-0.25</td>
<td>0.07</td>
<td>-3.55</td>
</tr>
<tr>
<td>Relative humidity</td>
<td>0.15</td>
<td>0.12</td>
<td>1.27</td>
</tr>
<tr>
<td>Relative humidity trend</td>
<td>-0.14</td>
<td>0.09</td>
<td>-1.53</td>
</tr>
<tr>
<td>(Relative humidity trend)$^2$</td>
<td>-0.16</td>
<td>0.06</td>
<td>-2.71</td>
</tr>
<tr>
<td>(Eastward wind $\times$ Northward wind)</td>
<td>0.13</td>
<td>0.09</td>
<td>1.55</td>
</tr>
<tr>
<td>Best four-layer lifted index $\times$ Air pressure trend</td>
<td>0.14</td>
<td>0.10</td>
<td>1.44</td>
</tr>
<tr>
<td>Latitude of breeding area</td>
<td>-0.12</td>
<td>0.11</td>
<td>-1.03</td>
</tr>
<tr>
<td>Migration distance</td>
<td>0.17</td>
<td>0.12</td>
<td>1.42</td>
</tr>
</tbody>
</table>
were temperature in May and precipitation in July. The former was negatively related to the proportion of juveniles, whereas the latter was positively related and stabilized in the presence of high precipitation (Table 2, Fig. 4). Age ratio was also higher in the presence of high
temperature and precipitation in June. Overall, climatic variables on the breeding grounds explained 65% of the observed variation in age ratio (calculated from the deviance ratio of the model including only the factor 'source of data'). In contrast, the models accounting for weather conditions during migration only explained 10% (non-linear shifted migration), 15% (linear shifted migration) and 37% (non-shifted migration) of the variation in age ratio (Tables S3_1 to S3_3 in Appendix S3). More importantly, the main weather variables correlated with age ratio were not the ones that were strongly related to migration movements. In particular, coefficients estimated from air pressure and air pressure trend exhibited high uncertainties (Table 1).

Early-brood ratio was quite similar between hunted and ringed individuals in France \( (r = 0.48, n = 21 \text{ years}) \). Values in the Russian data were slightly higher (Fig. 3b) but between-year variation was high, so selection based on AIC favoured models without the factor 'type of data' (Table S4_1 in Appendix S4). The lowest AIC in the models examining early-brood ratio was achieved by a model accounting for weather conditions under the hypothesis of non-shifted migration. Air pressure and relative humidity showed negative correlations with early-brood ratio (Table 3), but their effects on migration movements had high uncertainty (Table 1, Appendix S2). The models evaluated under the alternative hypotheses of linear and non-linear shifted migration phenology performed poorly (Appendix S4). Of the climatic variables extracted at the breeding grounds, only temperature in May was selected. Early-brood ratio was higher in the presence of higher temperatures in May.


**Table 2.** Estimated parameters of the best model fitting age ratio to the climatic variables at the breeding grounds (see Appendix S3 for other models, all having \( \Delta \text{AIC} \gg 2 \)).

<table>
<thead>
<tr>
<th>Covariates (scaled)</th>
<th>Estimated coefficients</th>
<th>Estimated standard errors</th>
<th>t-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>59.27</td>
<td>0.83</td>
<td>71.41</td>
</tr>
<tr>
<td>Source: ringed in Russia</td>
<td>16.94</td>
<td>3.40</td>
<td>4.98</td>
</tr>
<tr>
<td>Source: hunted in France</td>
<td>7.35</td>
<td>0.73</td>
<td>10.07</td>
</tr>
<tr>
<td>Temperature May</td>
<td>-2.50</td>
<td>0.41</td>
<td>-6.10</td>
</tr>
<tr>
<td>Precipitation July</td>
<td>2.89</td>
<td>0.40</td>
<td>7.22</td>
</tr>
<tr>
<td>Precipitation June</td>
<td>1.69</td>
<td>0.41</td>
<td>4.12</td>
</tr>
<tr>
<td>Temperature June</td>
<td>0.75</td>
<td>0.45</td>
<td>1.67</td>
</tr>
<tr>
<td>(Temperature June)²</td>
<td>1.57</td>
<td>0.37</td>
<td>4.24</td>
</tr>
<tr>
<td>(Precipitation July)²</td>
<td>-1.54</td>
<td>0.46</td>
<td>-3.35</td>
</tr>
<tr>
<td>( P: 0.80 )</td>
<td></td>
<td>AICc: 397.2</td>
<td></td>
</tr>
</tbody>
</table>

**DISCUSSION**

**Migration movements**

Spring migration movements of Eurasian Woodcock were clearly associated with particular weather conditions. Air surface temperature showed the strongest positive correlation, but wind, atmospheric stability and relative humidity trend were also highly related to migration movement probability (Fig. 2). Many studies of bird migration have shown that temperature has a major role in migration schedules (e.g. Marra et al. 2005, Hüppop & Winkel 2006, Gordo 2007, Tøttrup et al. 2010). Woodcock in particular avoided moving when temperatures were below or near 0 °C, and migration movement frequency reached 50% above 4 °C and 80% above 11 °C. Temperature may have an indirect effect on migration movements, i.e. increasing food abundance and availability at new sites along the migration route, which consequently stimulates birds to continue their travel. This would be analogous to the green wave hypothesis for goose migration (Si et al. 2015, and references therein).

Wind is also known to be an important factor influencing migration movements (Liechti 2006, Sinelschikova et al. 2007). Biologging technologies permitting the tracking of birds throughout their migration travels have recently highlighted the importance of this variable at the individual level (Conklin & Battley 2011, Safi et al. 2013). In our study, wind direction and strength were strongly correlated with spring migration movements of Woodcock (Fig. 2), with individuals logically taking advantage of tailwinds. Intriguingly, the effect of northward wind was much stronger than the effect of eastward wind, although there was no apparent advantage to Woodcock in heading north faster. Wind speed and direction may not only facilitate migration flights but may also provide some information on conditions at the following stopover sites. In particular, northward winds may give important information about temperature trend (and snowmelt) at a broad scale, whereas eastward winds are associated with rainy weather and atmospheric instability (which may generate snow when reaching cold areas). Another explanation might be related to the structure of winds in the different layers of the atmosphere. Indeed, birds may adapt their flight altitude by a compromise between wind support and air temperature (Kemp et al. 2013). We need reliable data on the flight altitude of tracked Woodcock to investigate this hypothesis.

Atmospheric conditions have not often been shown to influence non-soaring bird migration (Richardson 1990b). Yet, in theory, stable atmospheric conditions could also be advantageous for flapping-flight migration by reducing turbulence in the air and the risk of encountering storms, thus encouraging the bird to migrate. Atmospheric stability was evaluated here by the best four-layer lifted-index and was the third most important variable (after temperature and wind) explaining Woodcock spring migration movements (based on estimated coefficients, Table 1). Moreover, as expected, Woodcock migration movements were lower when relative humidity increased. We were unable to find any study in which this variable has previously been related to migration movements. Both atmospheric stability and relative humidity trend should thus be given greater consideration in future studies modelling bird migration movements.

Migration movements of Woodcock still occurred when weather conditions were not optimal. Indeed, the movement probability was rarely lower than 0.2 for each single effect (Fig. 2). Thus, it seems that only a combination of unfavourable elements could drastically reduce migration movement probability towards zero and, conversely, just a few favourable factors could encourage some birds to continue spring migration. A large amount (88%) of the observed variance (evaluated from the null model with only the individuals
considered as a random effect) remained unexplained by the best model. A part of this unexplained variance may be related to the accuracy of the variable used in the model. In particular, some variables may have spatial variation in their accuracy according to the density of weather stations, which may create additional variance or even bias in analysis (Baker et al. 2017). Another part of this unexplained variance results from variables and processes unaccounted for in the models. For instance, energy expenditure and body condition could affect the decision of Woodcock to stop or fly on at the individual level throughout the migration. Variables related to visibility (cloud cover and cloud-ceiling height) were not shown to affect Woodcock migration movements.

We found no difference in migration movements between juvenile (second calendar year) and adult Woodcock (third or more calendar year). However, Woodcock breeding further east had a higher rate of migration movements than birds breeding closer to the wintering grounds (Table 1). This is mainly related to the migration distance the birds have to cover, as the longitude

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**Table 3.** Estimated parameters of the best model fitting early-brood ratio to the weather conditions under the hypothesis of non-shifted migration phenology (see Appendix S4 for other models, all having ΔAIC > 2).

<table>
<thead>
<tr>
<th>Covariates</th>
<th>Estimated coefficients</th>
<th>Estimated standard errors</th>
<th>t values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>63.89</td>
<td>0.47</td>
<td>135.94</td>
</tr>
<tr>
<td>Air pressure</td>
<td>−1.98</td>
<td>0.45</td>
<td>−4.4</td>
</tr>
<tr>
<td>Relative humidity</td>
<td>−1.56</td>
<td>0.47</td>
<td>−3.32</td>
</tr>
<tr>
<td>(Air pressure)²</td>
<td>−0.97</td>
<td>0.30</td>
<td>−3.23</td>
</tr>
<tr>
<td>R²: 0.33</td>
<td></td>
<td></td>
<td>AICc: 379.01</td>
</tr>
</tbody>
</table>

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of the breeding area is highly correlated with the distance between the wintering and breeding areas ($r = 0.97$, $n = 82$ spring travels, ΔAIC of the alternative model = 1.1, see Appendix S2). Woodcock breeding further east and undertaking longer migrations thus compensate for their long-distance travel by increasing their rate of migration movement. Migration will have a greater impact on the fitness of these individuals, and they may need to be more efficient at finding resources at stopover areas and/or their breeding grounds might be expected to be of higher quality.

**Age and early-brood ratios**

Age ratio was higher among hunted Woodcock than those captured for ringing, but both trends across years were very similar. The higher age ratio among hunted birds is likely to be due to differential distribution of young birds according to hunting pressure, such that young birds reaching wintering areas for the first time are more likely to settle in hunted areas by accident than are adults, which almost always returned to the same wintering location (Fadat 1991). Once accounting for the factor ‘source of data’, annual age ratio was mostly related to climatic variables on the breeding grounds. Conversely, weather conditions during spring migration were unlikely to influence the proportion of juveniles. Temperature in May and June and precipitation in June and July showed strong correlations with age ratio. In May, most female Woodcock on the Russian breeding grounds are incubating, so a higher temperature might be construed as good for breeding. However, temperature and precipitation were positively correlated in May ($r = 0.43$, $n = 23$ years) and heavy precipitation might reduce hatching success. The negative correlation between age ratio and temperature in May suggests that unstable weather in May (high temperatures and precipitation) was detrimental to hatching success. Conversely, in June, most young would have hatched and would benefit from high temperatures and precipitation, which was consistent with the correlations we found. In July, dry weather will probably drive earthworms deeper into the soil and make it harder for Woodcock to probe, which could prevent them from feeding on soil invertebrates (Peach et al. 2004, Hoodless & Hirons 2007). Low rainfall in July could particularly affect Woodcock chicks, most of which will be full grown by July but still relatively naïve foragers, and could thus increase post-fledging mortality. Guzmán and Arroyo (2015) also showed a negative effect of temperature in July and a positive effect of precipitation on relative Woodcock abundance in Spain during the following winter, which would be partly related to the breeding success that summer. However, they also found a positive effect of precipitation in May, but did not provide interpretation of this result.

We evaluated breeding success using the age ratio, which only gave the proportion of young Woodcock in the population a few months after the breeding period. The limitations in the interpretation of results on age ratio must be borne in mind because, although breeding productivity will have a strong influence on age ratio values, conditions during autumn migration may affect adults and juveniles differently, e.g. differential mortality and/or migration routes. The abundance of Woodcock in Western Europe in a given winter is likely to depend strongly on weather conditions (especially frost) in northern and eastern countries, which push Woodcock towards southern areas such as Spain (Péron et al. 2011). Unfortunately, this was not taken into account by Guzmán and Arroyo (2015), and hence the relative importance of breeding ground conditions and autumn/winter weather (and their correlations) on the abundance of wintering Woodcock still need to be evaluated.

In contrast to age ratio, the early-brood ratio was poorly related to the covariates studied. The weather variables during spring migration that were correlated with early-brood ratio were not those correlated with migration movements. Such inconsistencies were probably due to multicollinearity between the covariates measured during spring migration and other important variables unaccounted for in our models. Of the variables extracted on the breeding grounds, only temperature in May may have a weak positive influence on early-brood ratio. This is plausible, as high temperatures in May advance spring phenology and hence hatching date (Hoodless & Coulson 1998). However, because temperature in May was negatively correlated with age ratio, it might produce antagonistic effects on breeding success and breeding precocity.

**Implications for population dynamics**

In a recent review, Shamoun-Baranes et al. (2017) provided an overview of the effect of atmospheric conditions on bird migration at the individual level.
and gave some insights into the consequences of these conditions at the population level. The authors highlighted that the feedback of weather conditions experienced during migration on population dynamics has not yet been sufficiently investigated. We have shown that the weather conditions experienced during spring migration had little influence on breeding success (age ratio after the breeding period) or breeding phenology (early-brood ratio) of Woodcock. Breeding success was mainly correlated with climatic variables on the breeding grounds, which could influence both hatching success and the survival of juveniles. Population dynamics of Eurasian Woodcock wintering in Western Europe are thus more likely to be related to the conditions on the breeding grounds than to conditions experienced during the spring migration, which is consistent with the income breeding strategy of this species (Stephens et al. 2009). Although many studies have examined carry-over or delayed effects of previous conditions on breeding success, most have also concluded that conditions on the breeding grounds were the most important (Legagneux et al. 2012, Ockendon et al. 2013, but see Finch et al. 2014).

Although spring migration weather conditions were not shown to affect breeding success of Eurasian Woodcock wintering in Western Europe at the population level, they could affect the fitness of birds at the individual or sub-population level. Indeed, indices used here reflected what was happening on average, but may have hidden differences between individuals or between geographical regions. Breeding success should ideally be evaluated at the individual level to assess further its link with spring migration conditions. In particular, birds breeding further from their wintering areas (east of the Ural Mountains) would theoretically be the most impacted by weather conditions during migration. These birds represented a small proportion of the population studied here, probably because of evolutionary processes exerting selection pressure on migration (Bell 2000, Liedvogel et al. 2011, Shamoun-Baranes et al. 2017). However, the proportion of these long-distance migrants is higher than previously thought (see Bauthian et al. 2007). It would be interesting to evaluate whether their occurrence in winter in Western Europe has changed over recent decades and, if so, why.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details on the weather variables used to study migration movements.

Appendix S2. Covariate selection, parameter estimates and model averaging for migration movement probability.

Appendix S3. Covariate selection and parameter estimates for age ratio.