

# Reduced Breeding Success Suggests Trophic Mismatch Despite Timely Arrival in an Alpine Songbird

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## Research Article

**Keywords:** avian migration, spring phenology, prelaying interval, reproduction, light-level geolocation, habitat, mountain, climate change, citizen science, remote sensing

**Posted Date:** January 5th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-137126/v1>

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# Abstract

A steady advance in the onset of spring is one of the most prominent footprints of climate warming and requires organisms, including migratory birds, to adapt their annual routines. As lower trophic levels typically adapt faster than higher trophic levels, observations of reduced fitness due to trophic mismatches are becoming more frequent, especially in long-distance migratory birds.

We aimed to identify key phenological events, and quantify potential mismatches and their consequences in a migratory songbird population of the Northern wheatear (*Oenanthe oenanthe*) breeding at high elevations in the European Alps.

We used light-level geolocators to track wheatears, and collected information on individual breeding activity and breeding success as well as environmental conditions during the reproductive season. In addition, we used citizen science data and remote sensed images to quantify longer term phenological trends.

Snow melt and green-up showed an exceptionally early spring in the study region in 2020, preceded by a relatively average year in 2019. Yet, tracked individuals arrived well before the snowmelt in 2020 and clutch initiation dates across the population were earlier in 2020 compared to 2019. However, this shift lagged behind the advance in environmental conditions. While hatching success was similar in both years, fledging success and overall nest success was significantly reduced in 2020.

Our results show that, despite the timely arrival at the breeding grounds, wheatears did not advance breeding activities in synchrony with environmental conditions during the exceptionally early year in 2020. The reduced fledging success suggests a trophic mismatch. However, the underlying mechanisms for hatchling mortality and nest failure remain unknown.

Earlier reproductive seasons are expected to become more frequent in the future. We show that the negative effects of changing seasons in Alpine migratory birds might be similar to birds breeding at high latitudes, despite their shorter migratory distance.

## Introduction

In migratory species, earlier availability of seasonal key food resources <sup>1</sup> generally leads to advancement in the timing of migration <sup>2</sup>. However, migratory animals often lag behind the advancement of lower trophic levels at the breeding site <sup>3</sup>. As a consequence, increasing phenological asynchronies <sup>4</sup> and trophic mismatches between consumers and their food resources are becoming more evident <sup>3,5</sup>. The reduced availability of food during offspring rearing that is often the result of a trophic mismatch can impact offspring growth <sup>6</sup>, survival <sup>7</sup> and recruitment in following years <sup>8</sup>. Given that those factors impact population trajectories, trophic mismatches are considered as among the greatest threats of climate warming on animal populations <sup>9</sup>.

In long-distance migratory birds that breed at high latitudes of the northern hemisphere and depend on highly seasonal food resources, trophic mismatches appear to be most prominent<sup>6</sup>. Long-distance migrants have also experienced stronger population declines over recent decades<sup>10,11</sup>. In contrast, shorter distance migrants seem to have higher flexibility in adjusting their arrival dates, and long-term studies have shown that bird populations that match the pace of changing climate and underlying resources can even have positive population trajectories<sup>12</sup>.

The Northern wheatear (*Oenanthe oenanthe*, henceforth wheatear) has one of the largest breeding distributions amongst migratory songbirds, ranging from Canada across all of Europe, Asia and into Alaska<sup>13,14</sup>. The non-breeding distribution is, however, confined to northern sub-Saharan Africa<sup>15-17</sup>. Thus, migratory distance in wheatears can vary between 3.000 and almost 15.000 km<sup>15,18</sup>. European Alpine breeding wheatears represent an interesting study population. For one, relative to other wheatear populations, they are amongst those with the shortest migratory distance from breeding to wintering grounds (approx. 3.500 km). However, the high-elevation breeding sites are, to some extent, comparable with those of the more northerly breeding populations; alpine breeding grounds are characterised by strong seasonal climate and food resources, and the duration of snow cover and the short season limits the reproductive period and requires accurate timing of life-history events<sup>19,20</sup>. The similarity is also reflected in life-history traits, such as a single clutch per year, of the wheatear subpopulations (*leucorhoa*) and the southern Alpine populations<sup>13,16</sup>. Like the northern seasonal regions, habitats in the European Alps have experienced marked changes over the last decades, including earlier springs indicated by an advance in bud burst<sup>21</sup>, and a prolonged snow free period<sup>22</sup>. However, most studies in Alpine habitats have focused on elevational shifts and habitat retraction as an effect of climate warming<sup>23,24</sup>, showing potentially strong negative impacts on birds occupying open grasslands<sup>25</sup>. Nothing is yet known or has pointed towards similar trophic mismatches between migratory birds and their food in Alpine habitats as observed at higher latitudes<sup>26</sup>.

The generally shorter migratory distances of Alpine breeding birds and the higher potential to adjust the timing in synchrony with lower trophic levels may reduce the risk of trophic mismatches. Alpine breeding individuals may have always arrived in advance or stayed at nearby stopovers to monitor environmental conditions and occupy their breeding sites as soon as conditions permit<sup>20</sup>, thereby buffering effects of recent earlier springs in the Alps.

A late snowmelt in 2019 and an exceptionally early snowmelt in 2020 across the European Alps provided a natural experiment that allowed us to explore the extent to which Alpine breeding wheatears experience a trophic mismatch in years when the season is advanced. We used light-level geolocators to track wheatears, and collected detailed information on individual breeding activity and success as well as environmental conditions during the reproductive season. In addition, we used citizen science data and remote sensed images to quantify longer term trends in the timing of wheatear migration and of environmental conditions, thus putting the data from our study area in a wider context. We predict that the relatively short migration distance of Alpine breeding wheatears leads to early arrival at the breeding

grounds, allowing reproduction in synchrony with environmental conditions, even in the exceptionally early year of 2020.

## Results

### Environmental conditions

The time series of the snow free date within the study area (Fig. 1a) from 2000 to 2020 showed high interannual variation, but no significant trend over time ( $t_{1191} = 1.88$ ,  $p = 0.059$ ,  $0.20$  days/year;  $-0.002$ – $0.419$  95%CI) (Fig. 1b). In 2019, the median snow free date was close to the long-term average, whereas the snow free date in 2020 was the earliest for over a decade (Fig. 1b). On average and at the finer scale around the detected wheatear nests, the area was snow free two weeks earlier in 2020 (median = 130 doy; 40th to 60th quantile 125–143) compared to 2019 (155; 148–164) (Fig. 2a). Similarly, vegetation growth reached the 80% threshold 17 days earlier in 2020 (162; 156–167) compared to 2019 (181, 178–184), and was strongly correlated with the snow free dates ( $R^2 = 0.43$ ,  $p < 0.001$ ,  $t_{254} = 7.68$ ). Snow cover and vegetation height data from direct observations in the field matched remote sensed images (Fig. 2a, date of snowmelt and 80%-ndvi amplitude).

### Migration schedule and arrival dates

We retrieved 11 geolocators, of which 9 contained sufficient data for further analyses (6 Migrate Technology, 3 SOI, of 5 males and 4 females). 14 tagged individuals were resighted ( $n = 35$ , return rate: 40%) of which 13 were recaptured. Two individuals lost the device. 9 adults of the control group were resighted ( $n = 16$ , return rate: 56%). The frequency of return rate between tagged and control groups was not significant (Fisher exact test,  $P = 0.126$ ). Six tags recorded light levels for the full annual cycle. One tag stopped recording after arrival at the main wintering site (24EA). Two tags stopped recording during spring migration (24DK, 24EP). In total, we derived arrival dates at the breeding site from six tracked individuals (Fig. 2b, see for details supplementary figures S1a-c, tables S1a-b).

Individual tracks revealed relatively long stopovers (approx. 20–30 days) before crossing the Sahara desert in autumn and shorter stopovers (approx. 5–10 days) just before reaching the wintering sites (Fig. 3, see for details supplementary table S2, figures S1a,S1c). Spring migration appeared to be faster, with fewer and shorter stopovers (approx. 5–10 days) (Fig. 3, supplementary table S2, figures S1a-c) until the coast of the Mediterranean Sea and Sardinia was reached. Here, most (4 out of 6) wheatears stopped for a longer period (approx. 15–20 days, Fig. 3, supplementary table S2, figure S1a). The arrival period at the breeding site for all tagged individuals ranged from 13th April to 6th May 2020 (Fig. 2b, supplementary table S1a, figure S1b). The three males (BT795, BT800, BT801) were on average 13 days earlier than the three females (Fig. 2b, supplementary table S3).

Interannual variation in the timing of spring arrival/transition in the larger region of the study area (observations of wheatears in ornitho.it database) was high over the last ten years ( $R^2 < 0.001$ ), with an average arrival in 2019 (median doy = 119) and a rather late arrival in 2020 (median doy = 130) (Fig. 2b,

supplementary figure S2, table S1b). Observation dates differed from the geolocator arrival dates in 2020, with earlier arrivals of tagged birds (median doy = 118, supplementary table S1b).

### Breeding phenology and success

Lay dates in 2020 were 8 days earlier on average, although there was much variation, compared to 2019 (Fig. 2b; median doy 2019: 158, range: 147–198,  $n = 74$ ; median doy 2020: 150, range: 135–195;  $n = 53$ ). However, due to later arrival in 2020, the interval between arrival and breeding (arrival-breeding interval) was shorter in the early year of 2020 (20 days) than in 2019 (39 days) (Fig. 2b). The difference in days between the peak of the green-up (ndvi 80% of amplitude) and hatching was shorter in 2019 (difference in median dates: 5 days) than in 2020, where hatching was 12 days behind (Environmental conditions, Fig. 2b). The median hatch date was the same in both years (median doy: 175), but in 2020 we observed greater variability in hatch dates (range: 152–212) than in 2019 (range: 164–180). Breeding phenology dates of tagged individuals did not differ from those of the studied population, but sample sizes were low due to nest failures in 2020 (for two-sample tests and dates see supplementary table S1b).

The success rates (a, b) were lower in 2020 than in 2019 ( $\beta = -1.4$ , 95% CrI: -2.870 – -0.018,  $P = 0.05$ ). Even though the difference in hatching success between years was negligible (99% (0.98–1.00) in 2019 and 98% (0.93–0.99) in 2020), the probability that a hatchling would fledge differed significantly and was lower in 2020 (94% (0.85–0.98) in 2019 and 80% (0.59–0.92) in 2020,  $\beta = 2.38$ , 95% CrI: 1.754–2.996,  $P < 0.001$ ,  $N = 683$ , Fig. 4). The nest success model (c) showed a non-significant trend in success rate with 65% (0.54–0.76) in 2019 and 51% (0.38–0.64) in 2020 ( $\beta = -0.139$  (0.314–0.040),  $P = 0.12$ ,  $N = 126$ , Fig. 4, supplementary table S4).

## Discussion

In long-distance migratory birds, trophic mismatches are mainly attributed to the inability to advance spring arrival at the breeding grounds in synchrony with temporal shifts in resource availability<sup>4,8,27,28</sup>. While a growing number of studies provide evidence for such trophic mismatches, reports on the impacts on fitness are rare<sup>29</sup>. Despite having only two years of detailed data, we show that an exceptionally early spring can reduce reproductive success in a bird population with a relatively short migration distance.

The seasonal dynamics in the European Alps are changing; over the last decades the snow cover period has become shorter resulting in an increase in primary productivity during the summer<sup>22</sup>, and while we could not find a strong trend in the snow free dates within the very low resolution remote sensing data (MODIS ndsi) of the study area in the Western Alps in Piedmont, we found high interannual variations (Fig. 1b), with an average year in 2019 and a very early snow free date in 2020. Direct observations and high-resolution remote sensing data (Sentinel-2) allowed for a more detailed quantification of the differences between the two years, showing that snow melt, crucial for the clutch initiation<sup>30</sup>, and green-up of the vegetation, a proxy for food availability<sup>31,32</sup>, occurred about two weeks earlier in 2020 (Fig. 2a). These year differences set the scene to compare key phenological events, such as arrival, clutch initiation,

date of hatching and fledging, as well as breeding success as a measure of individual and overall population fitness.

Sightings of Northern wheatears arriving in and passing through the Piedmont and Aosta valley during spring migration did not show a significant advancement over the last decade. However, individuals migrating through the area can come from various wintering sites in Africa and can vary even more strongly in their destination that can range from central Canada to eastern Russia<sup>15,18</sup>. Population specific migration schedules and potential trends may thus be hidden in the sighting dataset. In fact, wheatears from Greenland (*O. o. leucorhoa*) have advanced their migration within the last three decades<sup>33</sup> and previous studies on a northern lowland population of the wheatear have shown a continuous trend towards earlier arrival at breeding sites<sup>34</sup>. Constant effort trapping data of wheatears stopping over on islands in the Mediterranean Sea has revealed a weak, but not significant, trend towards earlier passage during spring migration within the last 18 years<sup>35</sup>. More importantly, the tracked individuals provided exact arrival dates for 2020, showing that the studied population arrived with the major migration flow of wheatears in the region (Fig. 2b), and we therefore assume that the arrival dates of the studied wheatears were similar between the two years since the major migration flow did not indicate major differences.

During spring migration the tracked individuals stayed for relatively long periods at stopover sites in the Mediterranean region before making the final leg of their migration and arriving some weeks ahead of breeding (Fig. 2b, 3). This finding is in line with tracking studies of the Swedish lowland population<sup>36</sup>. It has been suggested that these longer stopovers after the Sahara crossing are used to assess the environmental conditions in Europe and could therefore be used to buffer interannual variation in the timing of spring. Similar patterns were found in migratory Horned larks (*Eremophila alpestris*) that performed long stopovers before reaching their high elevation breeding grounds<sup>20</sup>. In addition to a general adjustment in the arrival time, wheatears can adjust the arrival-breeding interval according to their arrival dates and spring progression<sup>34</sup>, strongly suggesting that, to some extent, wheatears are able to match their migration and breeding activities with local conditions and seasonally limited resources<sup>37</sup>.

Based on these findings and due to the relative short migration distance, we predicted that wheatears breeding in the European Alps arrive before the conditions become suitable for breeding and can therefore cope with early springs by advancing their clutch initiation date. While our predictions regarding the arrival seem true, and clutch initiation was earlier in 2020 compared to the later spring in 2019, the advancement and thus the adjustment in the arrival-breeding interval was only about 8 days compared to the two weeks of the advancement in environmental conditions (Fig. 2b). If we assume that the timing was optimal in 2019 and spring green-up provides a reliable proxy for the food resources, the population experienced a median trophic mismatch of about one week in 2020. While we cannot test these assumptions without data, the reproductive success can provide some initial insights.

While hatching success was similar between the two years, the probability that a hatchling fledged, i.e. became independent, was significantly lower in the early year of 2020, leading to a reduced reproductive output in the population (Fig. 4). While this points towards a trophic mismatch, since the differences

occurred during the most resource demanding period, we can only speculate about the underlying mechanisms of hatchling mortality. To identify food shortage, data on chick growth is necessary. However, trophic mismatches may also have indirect effects. In our population, most nest failures were caused by predation. Increased begging behaviour due to food shortage could make nests more obvious to predators<sup>38</sup>. However, due to cold snaps, predators may have higher energy demands in early spring years, leading to a greater predator activity and higher nest failure rate. Potentially colder days and even cold-snaps including snow and frost during the early season are more likely to occur in earlier years. This in general could negatively affect breeding success, via lower adult survival<sup>39</sup> and reduced reproductive success<sup>40-43</sup>, even if migrants match the advanced spring conditions. Harsh environmental conditions during the incubation period may also delay hatching, exposing the nest to predators for a longer period at the same time<sup>44</sup>. Disentangling these effects will be an important challenge for ongoing and future long-term studies that combine phenological data, breeding performance, chick growth and predation risk.

Here, we have shown that breeding success was reduced in wheatears breeding in the European Alps in an exceptionally early year and despite timely arrival. We expected that this timely arrival, before the conditions allow the onset of breeding, will buffer the effects of early springs. However, the adjustment via shortening the arrival-breeding interval might not be flexible enough, as birds seem to be unable to advance egg laying sufficiently and thus may need to arrive even earlier to have the same arrival-breeding interval as in average years. The arrival-breeding interval is needed for recovering after migration, territory choice and defence, and mating<sup>45</sup>, and arriving even earlier is limited by a trade-off between achieving good territories and matching the hatch date with the peak of resources on the one side, and a higher risk of potentially lowered survival for adults<sup>39</sup> on the other. Similar limits in timing have been found in long-distance migrating pied flycatchers (*Ficedula hypoleuca*), which do not seem to be able to advance arrival at breeding sites to the same extent as the advance of spring, but they lay eggs earlier. Nevertheless, the advance in lay dates still seems insufficient to track the advance of spring, which might be the result of the inflexibility in their migration schedule that is triggered by day length instead of temperature<sup>46</sup>. McDermott and DeGroot<sup>47</sup> analysed data on 17 migratory species, and found a positive relationship between earlier arrival at the breeding grounds and earlier breeding in four species, whereas in six species, the arrival-breeding interval shortened in warmer springs, as occurred in our Alpine wheatear population in 2020 (Fig. 2b). The decrease in breeding success in 2020 can potentially be related to both harsh weather conditions in early spring and to the mismatched peak in food resources. However, since the difference in hatching success was not as high as the difference in fledging success, we consider the trophic mismatch to be the more likely explanation for the reduced breeding success. Earlier reproductive seasons are expected to become more frequent in the future, and climate change effects are found to be especially severe in high latitudes and elevations. Despite the shorter migratory distance of Alpine populations, negative effects of changing seasons are expected, as commonly observed for birds breeding at high latitudes.

# Methods

## Study area

Data on environmental conditions, breeding phenology and breeding success were collected in 2019 and 2020 during the breeding season, from May to August, in Parco Naturale Val Troncea, 44°57'28"N, 6°56'28"E, Western Alps, Piedmont, Italy (Fig. 1a). The elevation of the study area varies from 1,560 m a.s.l. to 2,700 m a.s.l. and was located on a south-eastern slope. The landscape structure is characterised by forests (predominantly larch *Larix decidua*) with shrubby patches at the lower elevations, and larches interspersed with open grasslands at around 2,200 m a.s.l., followed by rocky areas above the treeline. The valley is used seasonally as pasture, and grazing cows influence the distribution and availability of potential open grassland habitat across all elevations <sup>48</sup>.

## Environmental conditions

To investigate the longer-term trends in the annual date of snowmelt ("the snow free date"), we used the remotely sensed MODIS (MOD10A1.006) Terra Snow Cover Daily Global 500 m dataset with recordings starting in 2000<sup>49</sup>. Daily values for all pixels ( $n = 68$ ) within the study area were extracted from Google Earth Engine <sup>50</sup> via the R package *rgee* <sup>51</sup>. For each pixel and each year, we identified the snow free date as the first date without snow that was followed by at least 60 days of snow free conditions, ignoring potential snow free periods within the winter.

To derive higher-resolution snow free dates for the actual nest sites in the study area during 2019 and 2020, we used the remotely sensed Sentinel-2 MSI MultiSpectral Instrument Level-2A dataset with a spatial resolution of 10 m <sup>52</sup>. On the Google Earth Engine Server, we first selected all images taken in 2019 and 2020 intersecting at least one of the nest sites. Next, we masked cloud pixels using the Sentinel-2 Cloud Probability layer and a probability threshold of 60. We then calculated the normalised differenced snow index (ndsi, Band 8 & 4) and the normalised vegetation index (ndvi, Band 3 & 11). For each nest site and each image, we extracted the mean ndsi and ndvi values of all pixels within a 10 m radius ( $n = 2-4$ ) around the nest. For each nest site and for both years, we fitted a smooth line (loess fit with span = 0.2 from the R package *stats*) to the ndvi and ndsi values over the day of the year, and extracted the day when the line fell below 0.1 ndsi and exceeded 80% of the ndvi annual amplitude.

In the field, snow cover and grass height, as proxies for the spring green-up (i.e. the seasonal development of new vegetation growth) were monitored throughout the two breeding seasons (see for details and sample sizes supplementary table S6). Data were collected using a standardised protocol for territory mapping. In summary, we defined four sectors above the treeline (total area: 161 ha), characterized by open grassland habitat, a variation in elevation (~ 700 m) and a high density of wheatear territories. We defined a route (~ 6 km in each sector) along which we defined habitat survey points separated by a distance of 200 m (6–8 points each sector, 30 in total). Territory mapping and habitat point surveys were conducted over five visits between 27th May and 21st July 2019. Following the protocol introduced by <sup>53</sup>,

positions of males were recorded with a GPS device during the period between sunrise and 12am and during suitable weather conditions. Habitat parameters were recorded at each of these points (covering an area of 200 × 200 m at habitat survey points and a 100 m radius around territory points) at each of the five visits. The territory mapping as well as the habitat point survey was repeated in 2020 over 5 visits between 14th May and 6th July.

### **Light level geolocation**

Males and females were trapped either at their nest entrance during chick feeding or with spring traps (using mealworm bait). In 2019, 35 adults were tagged, using 15 (8 males, 7 females) light-level geolocators manufactured by Migrate Technology Ltd. (Intigeo P65, light stalk, 0.8 g, fitted with a leg-loop harness<sup>54</sup> and 20 (10 males, 10 females) geolocators manufactured by the Swiss Ornithological Institute (SOI, SOI-PAM, light stalk, recording pressure, 1.1 g). Device weights were on average 4.1% of the individuals' body mass (2.8–5.2%, see supplementary table S5). All captured individuals were marked with three plastic colour rings and a metal ring of the Italian bird ringing scheme. As a control for the effect of geocator devices in return rates, an additional 16 individuals were banded, but were not fitted with a geocator. All animal handling and protocols were carried out in accordance with relevant guidelines and regulations under licenses issued by Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA, protocol no. 27303, no. 2463) and Città di Torino (license no. 56.1433/2019, no. 197.4765/2019).

Light-intensity data were recorded at 5 minute intervals and analysed using a threshold method<sup>55</sup>. Sunrise and sunset events (twilight events) were identified on log-transformed light data and a threshold of 1 log lux, using the R package TwGeos<sup>56</sup>.

Twilight events recorded at the known deployment site during periods after deployment and before recapture were used for calibration, i.e. to estimate the error distribution of twilight events and the individual reference sun elevation angle (position of the sun when twilight events were detected). For recordings from Migrate Technology Ltd. tags, migratory movements were identified as sudden and directed changes of consecutive sunrise or sunset events (for details, see “invMovement” method description in<sup>57</sup>). Stationary periods with a minimum of two consecutive twilight events were then identified as periods surrounded by migratory movements. For data recordings from Swiss Ornithological Institute tags, we used the additional air pressure measurements to identify movement periods with a change in pressure threshold of 4, using the method implemented and described in the R package PAMLR<sup>58</sup>.

For the final track estimation, we used a Bayesian approach from the R Package *SGAT*<sup>59</sup> allowing the incorporation of twilight events, their error distribution (gamma density distribution), the information on periods of movement and residency, a spatial probability mask and expected flight speed distribution (gamma distribution with shape = 2.2 and rate = 0.08).

The method provides the most likely paths with credibility intervals derived via Markov Chain Monte Carlo (MCMC) simulations. The applied *groupedThresholdModel* provides a single location estimate for stationary periods as well as one location estimate for each twilight during movement. A spatial mask was applied for the estimate of stationary locations, restricting positions to be estimated on land. During the MCMC simulation, the first and last site of residency (in case the logger was still recording light on return from the wintering grounds) were fixed to the deployment site.

We first ran a *modifiedGamma* model (relaxed assumptions) for 1000 iterations to initiate the model, before tuning the model with final assumptions/priors with three runs, each containing 300 iterations. Finally, the model was run for 2000 iterations to ensure convergence. Median location estimates and 95% CrI were calculated using the entire final MCMC chain (i.e. each location estimate was based on 2000 estimates from within the MCMC chains). Locations from the most likely track were used for plotting.

## Arrival Dates

We used three different approaches to estimate the timing of departure and arrival at the breeding grounds from the geolocator data. First, we used the dates from the above-described analysis of the stationary periods (first day at breeding ground after last northward migration stopover site, supplementary table S2). Second, we performed a separate analysis on the defined twilight times to estimate the probability that each sunrise and sunset time were recorded within the larger area around the breeding site (radius = 250 km). To this end, we used the calibrated individual gamma distribution of the twilight error and simulated 500 locations for each twilight time. The resulting locations reflect the expected precision of the location estimates (see <sup>60</sup>). The probability was then defined as the percentage of location estimates per twilight falling into the defined radius around the breeding site. A symmetrical Gaussian curve was then fitted to the probabilities over time, and departure and arrival was calculated as the date when the curve fell respectively below or exceeded the 0.5 probability (as well as the 0.025 and 0.975 probability to report the 95% confidence intervals). The idea behind the third approach emerged while inspecting the light recordings. During the sunrise periods at the beginning and the end of the recordings, thus at the breeding site, we discovered a time delay in the daily maximum light values. This was caused by the south-eastern slope of the breeding area and the fact that the direct sunlight was blocked by the mountain ridge in the east (Fig. 1a). To make use of this pattern in the identification of the exact arrival and departure time at the breeding site, we applied an additional calibration with a higher light intensity threshold (9 log lux), slightly below the maximum light values the tags can resolve (11 log lux) resulting in a gamma distribution of the delayed maximum light intensities. Due to the changes in the position of the sun, the delay is expected to change over the course of the year, thus we estimated the gamma distribution parameters for autumn and spring separately. Next, we calculated the probability that the daily timing of the maximum light intensity during sunrise would belong to the derived gamma distribution (first half of the light recordings were compared to the autumn gamma distribution and second half to the spring gamma distribution). A symmetrical Gaussian curve was then fitted to the probabilities over time, and departure and arrival was calculated as the date when the curve fell

respectively below or exceeded the 0.5 probability (as well as the 0.025 and 0.975 probability to report the 95% confidence intervals).

To estimate the general migration transition of wheatears migrating northwards from African wintering ranges into the wider area of the breeding site in the Western Alps (the regions Piedmont and Aosta Valley), we used citizen science data of wheatear sightings during spring submitted via the ornitho.it platform. The data includes the number of observations of wheatears per day in the period March-May in the years 2010–2020.

### **Breeding phenology and success**

From the fourth week of May until the first week of August (2019, 2020), we searched for wheatear nests in all four sectors as well as adjacent accessible areas, including open grassland sites at lower elevations (pastures). Each identified nest was marked with bamboo sticks at a distance of at least 5 metres, and consecutively monitored until the chicks fledged or the nest failed.

Depending on the stage (e.g., longer breaks during incubation when date of hatching could be estimated from date of laying the last egg, following <sup>13</sup>, the status of the nests was recorded on average every five days. In 2020, at each visit, habitat parameters at the nest were recorded. We were able to record the exact dates for building, laying, hatching and fledging for some nests in 2019 and 2020, and subsequently estimate the duration of each stage for our population (see for details supplementary table S7). We used the average of these individual durations of each stage (supplementary table S7) to estimate breeding phenology dates for nests where direct observation was not possible in all their stages (back or forward in time from a known breeding phenology date). If the number of eggs laid was unknown, we assumed a clutch size of five eggs, which is the average number within our population (nests reaching the stage of incubation and no. of eggs known, 2019: 36, 2020: 22), to estimate the lay date. Breeding phenology dates were calculated only for stages reached by the individual nest, e.g. we did not estimate a fledge date if the nest failed before. The arrival-breeding interval for both years was estimated by calculating the difference between the mean arrival date (from geolocation and ornitho.it) and lay date.

To estimate and compare the breeding success of the population between the two consecutive years 2019 and 2020, we considered three different measures: a) the hatching success rate (eggs that hatched), b) the fledging success rate (hatchlings that fledged), and c) the nest success rate (successful nests/all nest attempts) (binomial response). Measures a and b allowed us to separate the breeding success in two states of a nest, i.e. nests during incubation and nests during chick rearing, by considering the success rates of individual eggs and hatchlings estimated as probabilities of reaching the next state (“period” hatching and fledging).

We applied a general linear mixed model to quantify the success rate of hatching and fledging (a, b) with the fixed effects “year” (2019, 2020) and “period” (hatching, fledging), adding “nest id” as a random effect (using the function `glmer` from package `lme4` <sup>61</sup>). To quantify the nest success rate (c), we applied a

generalized linear model with the fixed effect “year” (using the function `glm` from package `stats`). Model assumptions were tested by drawing residual plots and checking for overdispersion (function `dispersion_glm` from package `blmeco`<sup>62</sup>). Conclusions from test statistics were based on the credibility intervals from the model predictions calculated using the function `sim` from package `arm` (Gelman, 2007), and by drawing 2000 random samples from the posterior distribution of the model parameters to obtain their 95% credible intervals from these simulations. An effect was considered significant if the credible interval of the model estimate did not include zero<sup>63</sup>.

## Declarations

### Acknowledgements

Thanks are due to Chris Fiedler, Ursula Scuderi and Liam Kelly who contributed to environmental data collection, nest monitoring and banding, including geolocator deployment and retrieval. We are also grateful to Heiko Schmaljohann for giving specific advice for fieldwork methods and trapping, to Michele Ottino and staff of the Ente di Gestione delle Aree Protette delle Alpi Cozie for logistical support, and Enrico Caprio and `ornitho.it` for providing the citizen science data. We further thank the German Ornithologists’ Society for supporting this project with a research grant (designated to MM Sander) to fund the Migrate Technology Ltd. geolocators. This work is a collaboration between the University of Turin and the Alfred-Wegener Institute Helmholtz Centre for Polar and Marine Biology in Potsdam, which was the hosting institute during data analysis and manuscript writing. The project was funded by the PhD internship of Martha Maria Sander during her period abroad.

### Author contributions

MMS, DC initiated the study. MMS, DC, CM, RA, SJ and DR collected the data. MMS, DC and SL conceptualised the manuscript. MMS and SL analysed the data. MMS and SL wrote the manuscript with significant input from DC. All authors approved the final version.

### Additional information

#### *Ethical statement*

The field work and data collection in Parco Naturale Val Tronca (Gestione Alpi Cozie) was authorized by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale, <https://www.isprambiente.gov.it/it>, protocol no. 27303, no. 2463) and Città di Torino (license no. 56.1433/2019, no. 197.4765/2019), which includes the capture, ringing and tagging (geolocators) of wheatears in the protected area in the period 2019-2021.

#### *Data availability*

Geolocator data including the raw light recordings, the annotated twilight files, the location estimates with credibility intervals and the R code will be uploaded onto Movebank ([www.movebank.org](http://www.movebank.org)) upon paper

acceptance. R code for Satellite data manipulation and Northern wheatear sightings can be accessed at [https://github.com/slisovski/Sander\\_et\\_al\\_Analyses](https://github.com/slisovski/Sander_et_al_Analyses) and will be uploaded to a public repository (Zotero) upon paper acceptance. Field observations including nest site occupation, clutch size, hatching and fledging success as well as snow and vegetation monitoring data is available upon request.

### ***Competing interest statement***

We declare that we have no significant competing financial, professional, or personal interests that might have influenced the performance or presentation of the work described in this manuscript.

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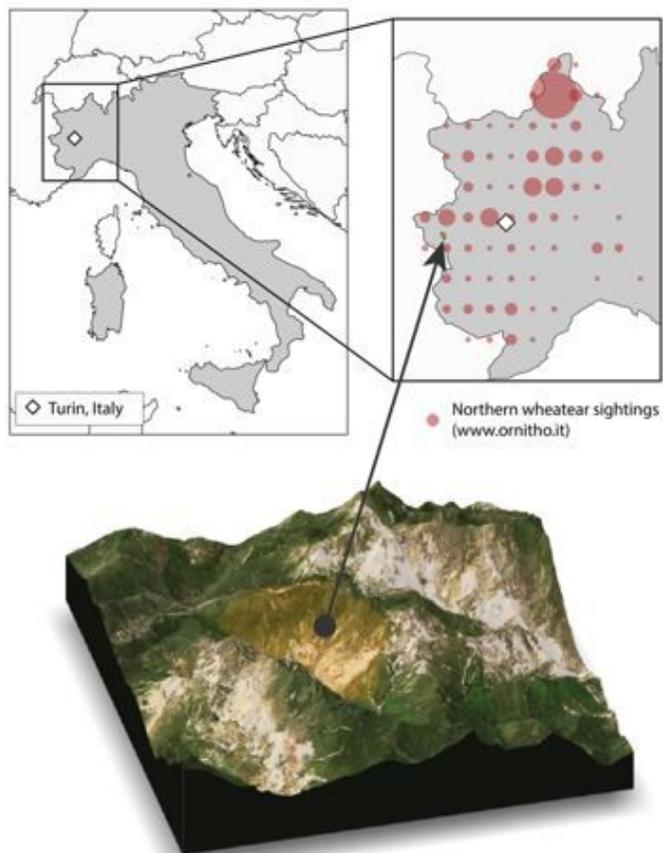
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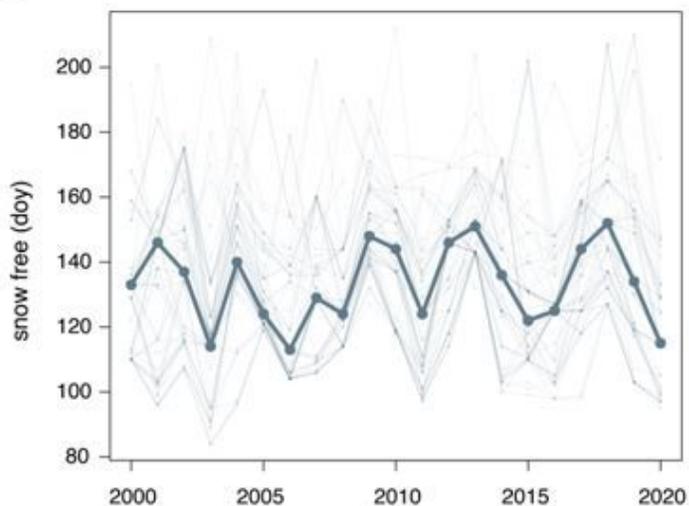
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# Figures

a)



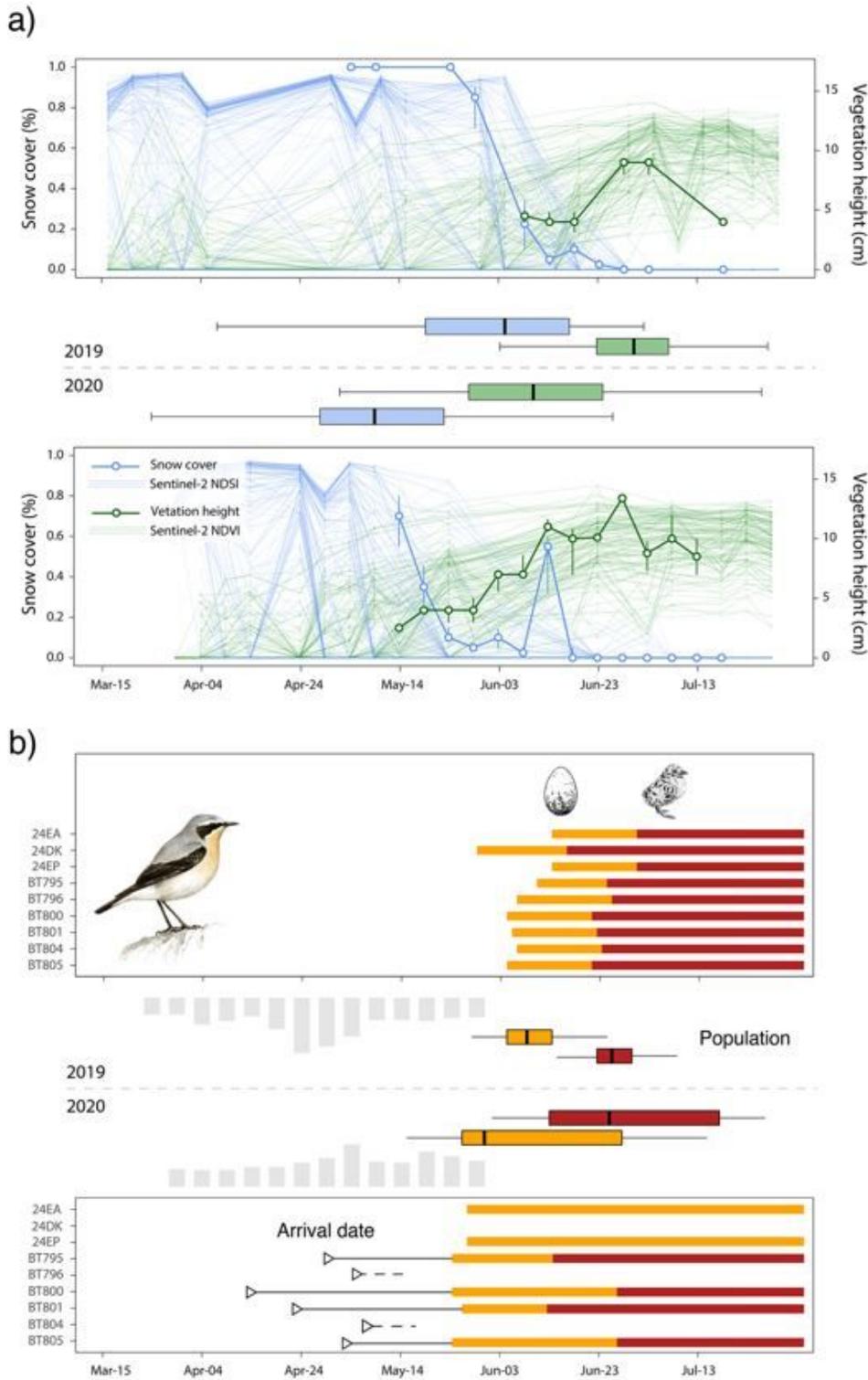
b)



**Figure 1**

a) Location of the study area, Parco Naturale Val Troncea in the Western Alps in Piedmont, Italy (yellow shaded south-eastern slope in topographical map), and the locations of wheatear sightings between March to May submitted to the ornitho.it database (red circle size corresponds to the number of sightings

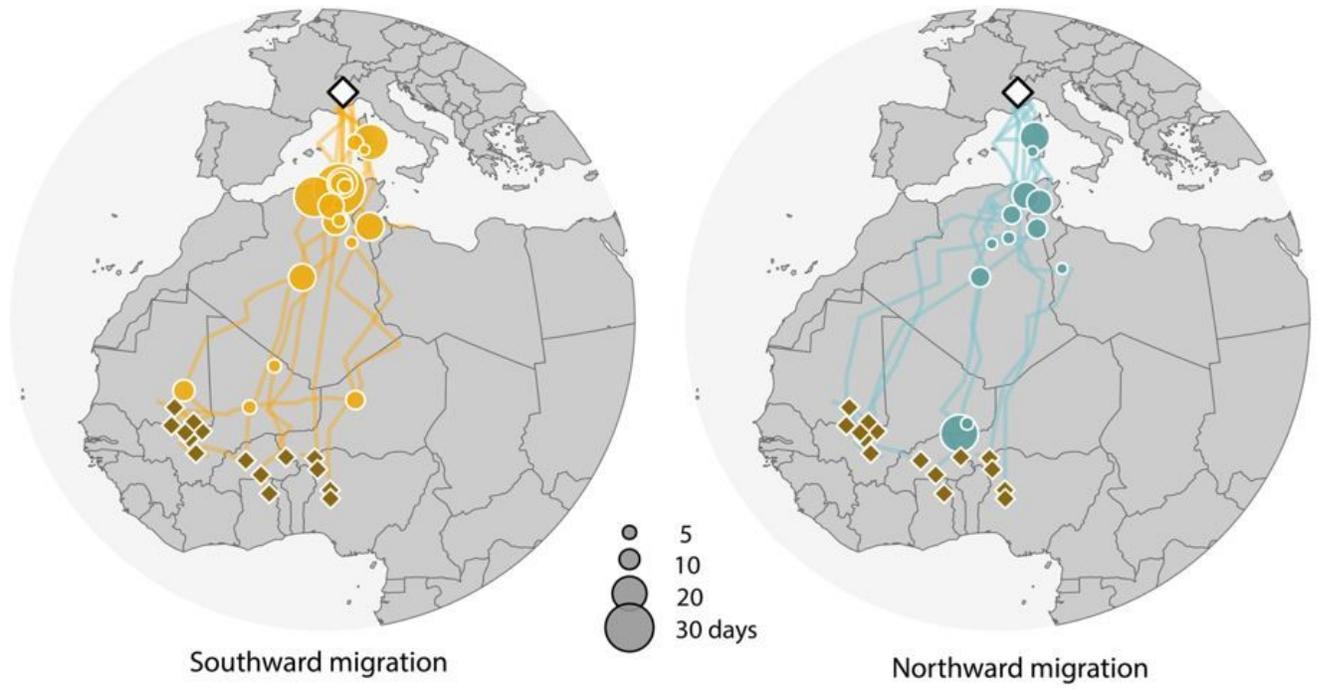
within a 0.25 degree grid cell). b) The day of the year, from 2000 to 2020, after which the study area was generally snow free in spring for at least 60 days. The fine lines represent the snow free dates for all MODIS satellite image pixels within the study area and the thick line connects the annual median values across pixels. Map data from Natural Earth ([naturalearthdata.com](http://naturalearthdata.com)), Landsat 5 and topographic model was downloaded from mapbox ([www.mapbox.com](http://www.mapbox.com)). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 2**

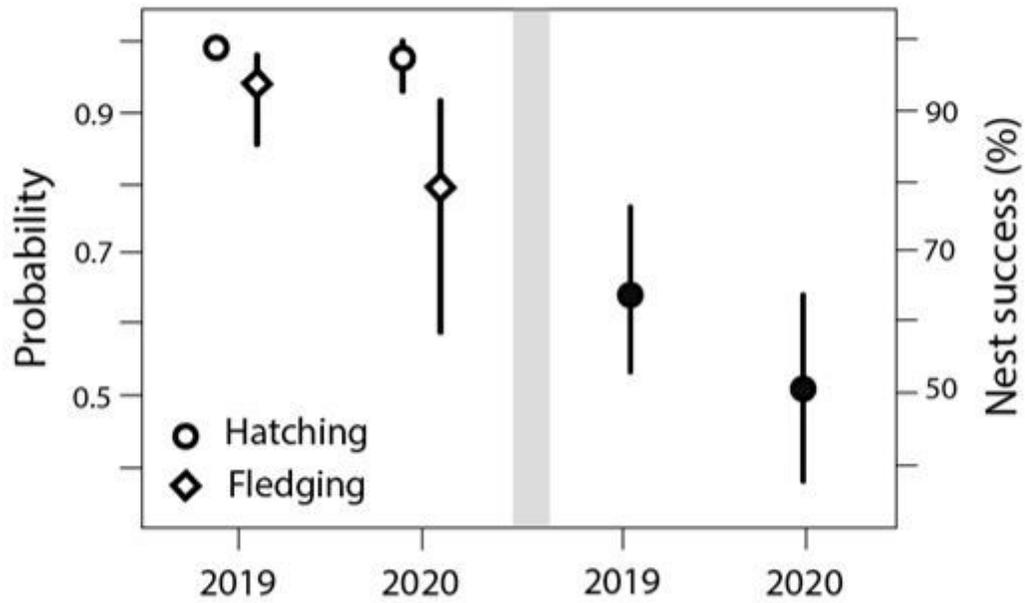
Arrival and lay dates at the Alpine breeding ground in relation to the spring green-up. a) Snow cover and vegetation height data derive from the territory, habitat (2019 & 2020) and nest monitoring (2020). Measures for the green-up derive from Sentinel-2 data: day of year when snow cover was less than 10% of the maximum and ndvi reached 80 % of the amplitude are shown in boxplots. b) Barplots (grey) show the no. of observations from ornitho.it in Piedmont and Aosta Valley from March to May. Triangles show

arrival dates of the tagged individuals (n = 6, 2020). Rectangles represent lay (orange) and hatch (red) dates of 9 tagged individuals (2019 & 2020), whereas the orange and red boxplots show the distribution of lay and hatch date across the whole population and season (nest monitoring 2019: n = 74, 2020: n = 53).



**Figure 3**

Most likely migration route estimates of individual Alpine breeding Northern wheatears. The breeding location is marked with a white diamond, stopover sites (>2 days) with an orange and blue circle, and wintering grounds with a brown diamond. Southward migration tracks include 9, and northward migration tracks 6, individuals. Map data downloaded from Natural Earth ([naturalearthdata.com](http://naturalearthdata.com)). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 4**

Left: Year effect on the probability of hatching (a) and fledging (b). Right: Year effect on nest success (c).

## Supplementary Files

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