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Short-term impact of an extreme weather event on the threatened Dupont's Lark *Chersophilus duponti*

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Summary

The frequency and intensity of extreme weather events represent a threat for biological diversity and are expected to increase in many regions over the following decades due to climate change. Our current knowledge about the impact of extreme weather events on the population dynamics of bird species is very limited. Here, we evaluated the impact of an extreme winter snowstorm on the abundance of 14 populations of the threatened Dupont's Lark *Chersophilus duponti*, a resident bird whose European population is restricted to Spain. We found a drastic and significant population decline in the next reproductive season following the extreme weather event. During the control period (2017–2020) the species suffered an overall annual decline of 19.4% (±5.0, SE). However, the overall annual decline after the storm was 67.6% (±9.4, period 2019–2021), with a mean decline of 66.5% (±15.9) for seven populations monitored both the year before and the year after the snowstorm (period 2020–2021). The snow covered the ground for over 10 days in central and eastern Spain, which together with a subsequent extreme cold wave could have reduced the species ability to find food resources and properly thermoregulate, forcing the species to move to unknown areas. Indeed a few days after the storm, several individuals were reported in areas typically avoided. Such displacements may increase the mortality risk for dispersing individuals, besides the direct effects of the extreme cold event, such as thermal challenges to energy balance or a reduced immune function. We discuss the potential role that extreme weather events may have on the population dynamics and conservation of the species.

Introduction

Climate change is recognised as one of the most important drivers of the current loss of biological diversity (IPCC 2014). To date, most studies on climate change have predominantly focused on the direct effects of rising temperatures (Thuiller 2007), increasing carbon dioxide levels (Meehl and Washington 1996), or sea-level rise (Runting *et al.* 2013). However, the indirect impacts of climate change on ecosystems, such as changes in hydrological cycles and increasing magnitude and frequency of extreme weather events (i.e. floods, droughts, and cyclones) have been less often analysed (Rahmstorf and Coumou 2011, Ummenhofer and Meehl 2017; reviewed by Maxwell *et al.* 2019). Climate influences all living organisms since individuals are adapted to occupy their niche according to their biological requirements (Soberon and Peterson 2005). Therefore, abnormal variations on climate will likely impact the survival, breeding success, and phenology of species (Crick 2004, Carey *et al.* 2009, Reichert *et al.* 2012, Maxwell *et al.* 2019). The frequency and intensity of extreme weather events are predicted to increase in many regions of the world due to climate change, creating a new threat for many species (Easterling and Karl 2001, Meehl and Tebaldi 2004, IPCC 2014, Maxwell *et al.* 2019). Indeed, understanding the impacts of extreme climatic events on populations and ecosystems is considered one of the factors of greatest importance to protect biological diversity (Sutherland *et al.* 2009).

Among the extreme climate events there are those associated with cold events, such as storms, snowfalls, and cold waves (extreme cold events hereinafter). Extreme cold events may pose a great risk for bird survival (Formenti *et al.* 2015, Krause *et al.* 2016), even when they are time restricted.

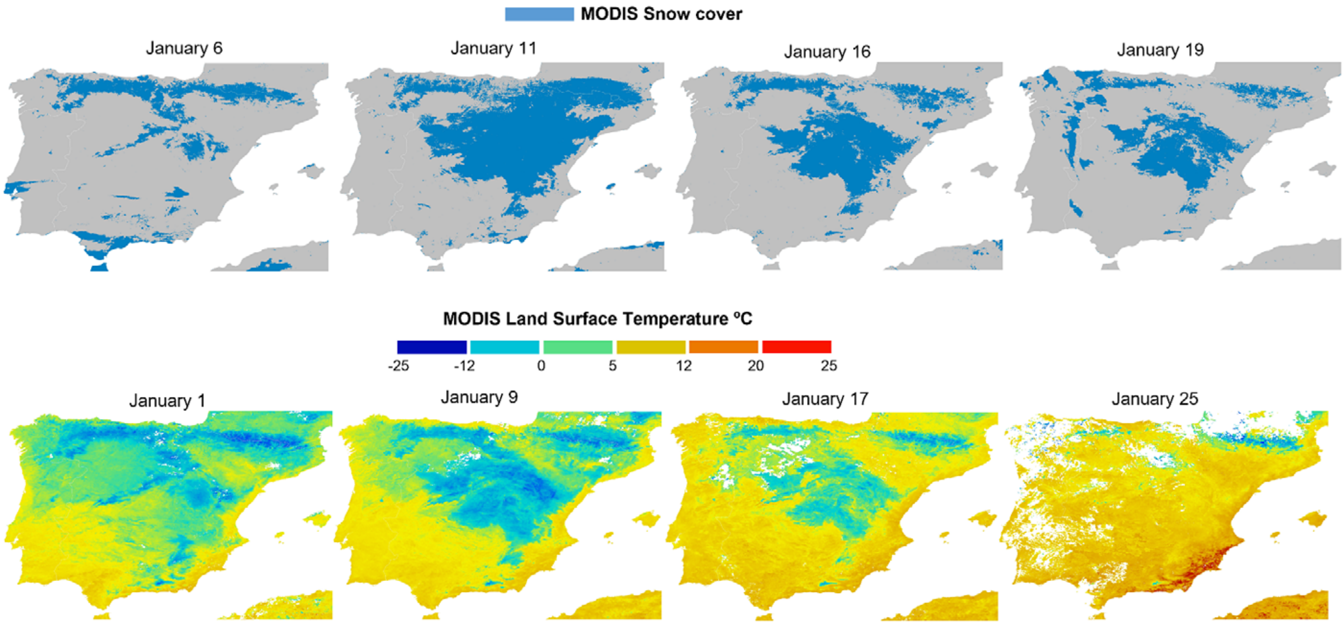

Figure 1. Evolution of the snow cover and land surface temperature in the Iberian Peninsula during Storm Filomena. The snow cover was extracted from the modis product MOD10A1 that provides a daily composite of snow cover at a 500-m spatial resolution. Land surface temperature was estimated from Modis 8-days product MOD11A2 that provides an average 8-day per-pixel land surface temperature and Emissivity (LST&E) with a 1-km spatial resolution. Temperatures below zero are represented by blue colours and temperatures above zero up to 25ºC are represented by green to yellow, orange, and red, respectively.

For example, Sanders *et al.* (2011) estimated that around 12% of a population of the threatened Carnaby's Black Cockatoos *Calyptorhynchus latirostris* were found dead after a two-hour storm. Nonetheless, the real impact was likely much greater since several individuals would have died but remained undetected (Sanders *et al.* 2011). Beyond the direct impact of extreme cold events on bird survival, previous studies have also found that cold events may directly limit food intake, cause thermal challenges to energy balance (Ramakrishnan *et al.* 2013), affect population dynamics via carry-over effects on breeding success in the subsequent breeding season (Järvistö *et al.* 2016), or create prolonged stress on birds (Rogers *et al.* 1993, Liu *et al.* 2018), which may suppress the immune function and health of the individuals.

The negative impact of extreme cold events on bird species may be enhanced on 1) those living at higher elevations, such as uplands, where the frequency and the intensity of extreme cold events are more pronounced (reviewed by Scridel *et al.* 2018), and on 2) smaller body passerines adapted to warmer conditions (Cohen *et al.* 2021). Similarly, species with a high degree of habitat specialisation might be more prone to being affected by extreme cold events, since generalist species usually occupy a wide range of habitats and feed on different kinds of food. Populations of specialists and threatened species are usually spatially isolated, which increases their vulnerability to stochastic and extreme weather events and reduces their dispersal ability among habitat patches (Bech *et al.* 2009, Fjeldså *et al.* 2012). Finally, the negative impacts of extreme cold events might be even worse for insectivorous birds, especially residents that are present year around, because these species might be unable to find food resources for a long period of time following a snowfall event, and consequently may be displaced (Rajchard *et al.* 2006, Scridel *et al.* 2018). However, our current knowledge on the impact of extreme cold events on population dynamics of resident insectivorous bird species is limited, since these events are stochastic and threatened species are intrinsically difficult to monitor.

In January 2021 Storm Filomena, one of the largest snowstorms in the last 50 years in Spain, hit a large part of continental Spain (Figure 1). The storm lasted from 7 January to 10 January 2021 and was followed by a cold wave the following week, from 11 January to 17 January 2021 (Smart 2021). Both phenomena, the snowstorm and the cold wave, were officially catalogued as historic meteorological events by the Spanish Meteorological Agency (AEMET 2021). The snowstorm covered the interior of the Iberian Peninsula with historically deep accumulations of snow. For example, the snow fell continuously over 30 hours in the city of Madrid (central Spain), leaving more than 50 cm of accumulated snow (Tapiador *et al.* 2021), which exceeded all historical events of the last century (Smart 2021). Indeed, the whole region of Madrid and the region of Castilla-La Mancha were also declared "catastrophe areas" by the national government, and several other regions in south, central, and eastern Spain were also highly affected by the snowstorm (Figure 1). There were snowfall accumulations of 50 cm in several areas of central Spain and about 25 cm in eastern Spain, such as in Zaragoza and the Ebro Valley (Rodríguez-Sánchez *et al.* 2021). The cold wave in the week following the snowfall was marked by minimum air temperatures between -5ºC and -15ºC in the most affected areas. The cold wave broke historical records of minimum air temperatures in several regions of Spain, with recorded official temperatures of up to -26.5ºC in Torremocha de Jiloca (Teruel province), but even lower temperatures (e.g. -33.6ºC in Checa-Vasequilla, Guadalajara province) at unofficial sites (AEMET 2021). Owing to the heavy snowfall and low temperatures during the preceding week, the snow lasted several days (up to two weeks in some areas) and caused major disruptions to daily life in Spain at the height of the COVID-19 pandemic (Smart 2021).

Currently, there is a need to assess the adaptive potential of birds and other organisms to unpredictable, extreme weather events as a result of climate change (Van der Pol *et al.* 2010). In this paper, we aim to document the short-term impact of extreme cold events, using Storm Filomena as a case study, on the abundance of an insectivorous, specialist, and threatened bird species in the breeding season following the storm. Given the increasing frequency and severity of extreme weather events over the world due to climate change, we hope our findings might be useful to better understand how extreme cold events may impact the population dynamics of birds.

Methods

Study species

We selected Dupont's Lark *Chersophilus duponti* as target species to assess the impact of extreme cold events on the distribution of birds. We chose that species because it is classified as a Vulnerable globally threatened insectivorous bird (Goméz-Catasús *et al.* 2018, García-Antón and Traba 2021, BirdLife International 2020) with limited dispersal movements and patchy distribution (Laiolo *et al.* 2017, Pérez-Granados *et al.* 2022). The European population of Dupont's Lark, which is restricted to Spain, has declined over 40% during the period 2004–2015 (Gómez-Catasús *et al.* 2018), and has been predicted to be extinct in two to three decades (García-Antón and Traba 2021). The current distribution of the species is extremely fragmented (García-Antón *et al.* 2020) and ranges from sea level up to 1,400 m a.s.l., although its main populations, such as those in the Iberian System and the Ebro Valley, are located above 1,000 m a.s.l. The fragmented distribution of the species is due to its strong dependence on flat, low shrub natural steppes (Garza *et al.* 2005, Pérez-Granados *et al.* 2017, Gómez-Catasús *et al.* 2019), a habitat type in decline in Iberia due to long-term habitat transformation. The species has been catalogued as resident (Suárez *et al.* 2006), overwintering above 1,000 m a.s.l., and defined as a poor disperser, with mean breeding dispersal movements around 100–150 m (Laiolo *et al.* 2007, Pérez-Granados *et al.* 2022). However, there are a few documented cases of individuals wintering outside their breeding areas and performing dispersive movements over 30 km (Suárez *et al.* 2006, García-Antón *et al.* 2015), which together with recent studies about metapopulations' connectivity (García-Antón *et al.* 2021), suggest that the species might be able to perform longer dispersals than previously thought. Indeed, Suárez *et al.* (2006) proposed that the whole population in a given area may perform temporal movements in response to exceptional weather conditions, such as heavy snowfalls. Due to its threat status, the extreme fragmentation of its optimal habitat, its small body size and aspects of its ecology (i.e. insectivory, ground-foraging behaviour, and poor ability to disperse), we considered Dupont's Lark to be an interesting model for the analysis of the impact of extreme cold events on a species at risk.

Bird monitoring

We collected data either annually or every two years for 14 Dupont's Lark subpopulations during the 2017–2021 period. We defined a subpopulation as all habitat patches separated by 5 km or less (following García-Antón *et al.* 2021). To facilitate reading we use the term population hereinafter. Surveyed populations covered most of the entire Iberian distribution of the species and hosted around 380 males in 2017 (c.10% of the European population) (Traba *et al.* 2019).

Dupont's Lark censuses were carried out during the breeding season (mid-March–mid-June). Birds were counted during the hour before sunrise by linear transect (500 m inner belt width) or territory mapping (three to four visits), during which vocalising males were annotated with the help of a GPS. Both counting methods produced very similar estimates (see Pérez-Granados and López-Iborra 2017). Estimated population size refers to the minimum number of males detected (line transect method) or territories defined (mapping method). Censuses were always performed under adequate weather conditions (e.g. no rain, low wind) and at constant speed. Each population was always surveyed by the same researcher team using the same counting method and repeating the same line transects throughout the study period, which allows inter-annual comparisons within the same population.

Statistical analyses

We estimated the population change of the monitored populations from the formula:

$$\text{Population change} = \left((N_\text{p}/N_i)^(1/\text{years} \right) - 1$$

where Np is the estimated population for one area for a specific year, N_i is the estimated population in the same area in the previous census, and years is the number of years between the estimates. These values were then multiplied by 100 to yield growth rates in percentages.

To assess the impact of Storm Filomena on the population dynamics of Dupont's Lark we estimated the mean population variation of the monitored populations for the following three periods: 1) control period (13 populations monitored between 2017 and 2020); 2) impact period (seven populations monitored the year before and the year after the storm, 2020 and 2021); 3) extended impact period (14 populations monitored two years before the storm and the year after, 2019 and 2021). We included the "extended impact period" to have an estimate of the impact of the storm on a larger number of populations. Whenever possible we used the largest elapsed time between censuses for the control period. For example, for those populations monitored annually, the annual variation for the control period was considered as the one that occurred between 2017 and 2020, while for the other five populations monitored during the control period the largest elapsed time was from 2017 to 2019 (see Table 1). To evaluate whether the population decline of Dupont's Lark was higher following Storm Filomena than during the control period, we fitted two one-sided Wilcoxon signed-rank tests (paired samples). We opted for a one-sided test since we hypothesised that the population decline would be higher owing to the storm impact. The first Wilcoxon test was run on the 13 populations for which there were data available to compare the population change during the control period with that obtained during the extended impact period, while the second test was fitted for only the seven populations with data available to compare the magnitude of change that occurred between the control and the impact period. The results are expressed as mean ± SE. The Wilcoxon signed-rank tests were conducted in R 3.6.2 (R Development Core Team 2019) using the *wilcox.test* function. The level of significance was P <0.05.

Results

The overall monitored Dupont's Lark population size decreased from 381 males in 2017 (one population first counted in 2019) to 146 males in 2021 (Table 1), with the local extinction of five populations following Storm Filomena, which represents 26.3% of the set of study populations (Table 1). The monitored populations suffered an average 19.4% decline during the control period

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Table 1. The number of Dupont's Lark males detected per year for each monitored population, as well as the population growth rate (in %) for the control period (2017–2020) and following Storm Filomena. For the rest of the monitored populations, the annual variation due to the impact of Storm Filomena was estimated with data collected two years before the storm (2019) and one year after (2021). The total number of males detected for the three years (2017, 2019, and 2021) when all populations were monitored is also given.

Population	Province	2017	2018	2019	2020	2021	Control %	Filomena %
(A) Barahona–Rello	Soria	139	91	97	73	86	−19.3	17.8
(B) Barcones–Marazovel	Soria	134	80	91	83	48	−14.8	−42.2
(C) Losar	Valencia	25	23	23	16	2	−13.8	−87.5
(D) Hontanar	Valencia	16	19	16	14	3	−4.3	−78.6
(E) Pinar	Valencia	9	4	2	1	0	−51.9	−100.0
(F) Alcubilla de las Peñas	Soria	7	7	3	2	0	−34.1	−100.0
(G) Cerrillo	Valencia	4	3	4	4	1	0	−75.0
(H) Alfés	Lleida	8	7	7	–	2	−6.5	−46.5
(I) Sierra del Picarcho	Murcia	10	8	12	–	0	9.5	−100.0
(J) Páramo de Corcos	Burgos	10	–	6	–	1	−22.5	−59.2
(K) San Frutos	Segovia	–	–	7	–	2		−46.55
(L) Conquezuela	Soria	3	–	2	–	1	−18.3	−29.3
(M) Esteras de Medinaceli	Soria	2	–	1	–	0	−29.3	−100
(N) Sierra Ministra	Soria	7	–	2	–	0	−46.5	−100
Total		374*		273		146		

*One population was not monitored.

(±5.0, SE, $n = 13$ populations), while the overall decline after Storm Filomena was 67.6% (±9.4, $n = 14$ populations monitored between 2019 and 2021). When considering only the seven populations monitored the year before and after Storm Filomena, the impact of the extreme weather event was even greater, with an overall decline of 66.5% (±15.9) (Figure 2). There was a significantly higher population decline following Storm Filomena than during the control period, both when considering the extended impact period (Wilcoxon signed-rank test: n = 13, Z = -3.33, V = 87, P <0.001) and the impact period (Wilcoxon signed-rank test: $n = 7$, Z = -2.27, V = 26, $P = 0.023$).

Discussion

In this study we found evidence of a drastic population change for the threatened Dupont's Lark following Storm Filomena, an extreme cold event. The year after the storm the monitored populations suffered a mean reduction of over 65%, which was more than three times higher than the mean decline observed during the control period and much higher than the average annual decrease estimated for a set of 92 Iberian populations during the period 2004–2015 (-3.9%) (Gómez-Catasús *et al.* 2018). The differences found in population annual variation between the control and the storm period were significant, and the extreme cold event also resulted in the local extinction of up to five small populations of Dupont's Lark. Although our dataset was limited, it comprised around 10% of the estimated European Dupont's Lark population. Therefore, we believe that our results, although not conclusive, may be representative of the impact of Storm Filomena on Dupont's Lark, whose entire population may have been heavily impacted. Our results are in agreement with previous studies which also found that extreme weather events may strongly impact bird populations in the short term (Sanders *et al.* 2011, Formenti *et al.* 2015, Krause *et al.* 2016).

Storm Filomena temporarily reduced habitat availability and the quality of several habitat patches occupied by the species, especially in high altitude areas, as habitat patches at higher altitudes were fully covered with snow for several days (Deshpande *et al.* 2022). According to official data provided by AEMET, there was snow cover for a mean of 11.1 days across the localities of the 14 populations included in the 2019–2021 dataset (mean of 10.8 days for the seven populations monitored in 2020 and 2021). The presence of snow cover for such an extended period likely caused a challenge for Dupont's Lark to find food resources due to the insectivorous habits of the species (Rajchard *et al.* 2006, Scridel *et al.* 2018). Indeed, the bulk of the diet is composed of terrestrial and hypogeal arthropods, such as spiders and beetles (Herranz *et al.* 1993, Talabante *et al.* 2015), which were covered by the snow during this period. Such limitations may have compromised the survival probability of the species and/or may have forced individuals to perform long spatial displacements looking for optimal habitats (i.e. lower altitude not covered by snow). In fact, there is some historical and recent data that reinforce this idea. In the winter of 1963, after heavy snowfalls at the inland Iberian Peninsula, several individuals of Dupont's Lark were observed in February at the Mediterranean coast far from any breeding population (Torredembarra, Tarragona province, north-eastern Spain), where they remained for several weeks (Mestre 1967). During Storm Filomena, on 13 January 2021, one Dupont's Lark was sighted at the Mediterranean coast (Marjal del Moro, Valencia province, eastern Spain) (Arribas 2021), where there are no known populations or previous records of the species within a radius of 100 km (Pérez-Granados and López-Iborra 2013). The bird remained in the area for around two weeks and afterwards it was not seen again. Another interesting record occurred in the urban area of the small village of

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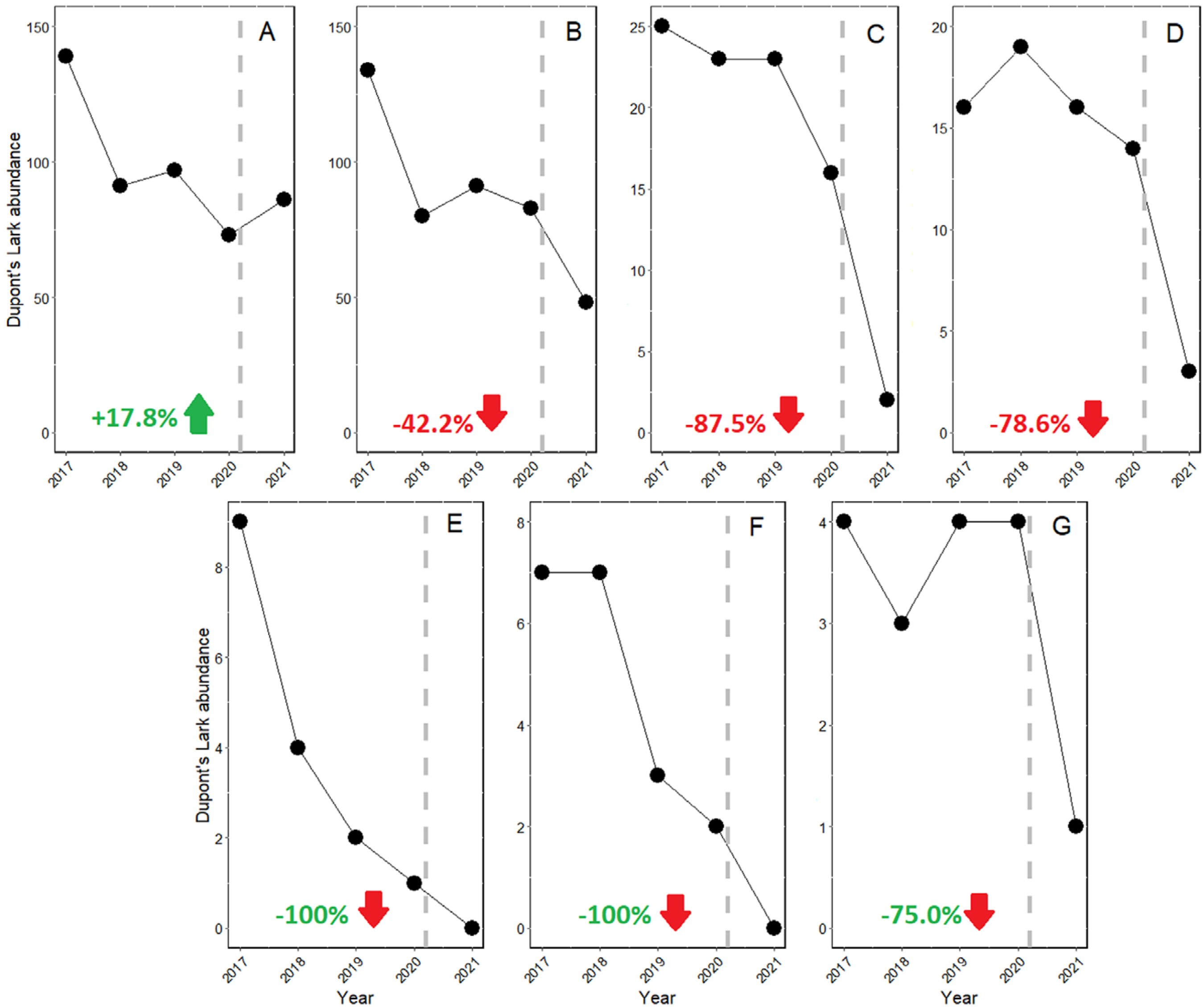

Figure 2. Estimated population sizes, in number of males, for seven populations of Dupont's Lark monitored annually during the 2017–2021 period. The vertical dashed line shows when Storm Filomena occurred, while the coloured numbers represent the population variation between 2020 and 2021. Letters identify populations as named in Table 1.

Tornos (Teruel province, central Spain, 201 inhabitants in 2021), where a ringed Dupont's Lark was found dead; this is a habitat typically avoided by this specialist species. This bird had been ringed in the preceding breeding season at Embid (Guadalajara province, central Spain), 24 km away. It has been suggested that the bird moved to feed in this urban area which had been cleared of snow (Fuertes 2021). These anecdotal records suggest that the species was forced to leave the breeding areas, at least temporarily, to non-optimal habitats, which may have compromised its survival.

Alarmingly the species suffered a mean annual decline of 19% during the control period, although it is in agreement with previous studies that also described the current decline of Dupont's Lark (e.g. Tella *et al.* 2005, Pérez-Granados and López-Iborra 2014, Gómez-Catasús *et al.* 2018). This declining trend threatens the persistence of the species by increasing the isolation and fragmentation of the remaining habitat patches. In 2018 the European Dupont's Lark population was estimated to be around 1,400–1,800 breeding pairs (Traba *et al.* 2019). These estimates could be corrected by applying a correction factor of 0.32 according to the mean decline of 68% owing to Storm Filomena. Therefore, the European Dupont's Lark population would be estimated currently to be around 448–576 breeding pairs. However, this estimate may have some uncertainties (e.g. due to the reduced number of regions and sampled sites for monitoring the impact of the storm), and further monitoring programmes are needed for estimating the European population size with increased accuracy.

Our results agree with Hendricks and Norment (1992) who found that a severe snowstorm had an important role in the population dynamics of the American Pipit *Anthus rubescens*, and the storm's impact was greater in small and peripheral habitat patches. We found that five small populations of Dupont's Lark (mean size 3.6 males, range 1–12) were extirpated after Storm Filomena. It is possible that the individuals comprising these small populations may have died due to the extreme cold event (e.g. thermal challenges to energy balance or reduced immune function), or that the individuals may have occupied a different habitat patch once they returned. For example, returning individuals may have selected to settle in occupied patches since the

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presence of co-specifics seems to guide migrating Dupont's Lark by advertising habitat quality (Laiolo and Obeso 2012). The recurrent impact of extreme weather events may negatively affect the meta-population dynamics of Dupont's Lark, given the small size of populations, and therefore proactive actions that aid the species in adapting to climate change (i.e. increasing habitat connectivity and intra-species genetic variation), which have been shown to benefit species threatened by extreme events, may be needed (Maxwell *et al*. 2019). Dupont's Lark populations may also benefit from more active actions, such as the translocation of individuals following successive extreme weather events (see a similar approach for flood events in Sousa *et al.* 2012). Indeed, the habitat of the only monitored population whose abundance increased after Storm Filomena, despite snow cover for the same amount of days (Barahona-Rello, Soria province, 73 males in 2020 and 86 in 2021) (Figure 2A), was actively managed during the spring of 2018 by the LIFE Ricotí programme. In that area the number of trees was reduced and extensive grazing was promoted to increase habitat availability and improve habitat quality for Dupont's Lark by increasing food availability associated with sheep dung (see Gómez-Catasús *et al.* 2021, Reverter *et al.* 2021). This preliminary finding suggests that active management of habitat patches focused on increasing habitat quality and availability might be a feasible solution to increase the viability of Dupont's Lark populations.

Besides the strong short-term negative impact of Storm Filomena on population dynamics, such extreme weather events could also have some positive impacts in the context of long-term population dynamics. Previous research suggests that extreme cold events may force Dupont's Larks to perform much longer movements than expected under normal conditions (Mestre 1967, Arribas 2021, Fuertes 2021), which might be particularly true for our target species, which have been defined as having low breeding dispersal ability (Laiolo *et al.* 2007, Pérez-Granados *et al.* 2022). It has also been shown in other bird species that extreme weather events, like strong winds, can result in colonisation of areas where they had not previously occurred (Cortés-Avizanda and Tavecchia, 2021). Future research should try to elucidate the role that extreme weather events may play in maintaining gene flow among Dupont's Lark populations (Méndez *et al.* 2011), or in local extinction and recolonisation processes in isolated populations such as the case observed in Catalonia, where Dupont's Lark was seen a decade after becoming locally extinct (Gómez-Catasús *et al.* 2018). These events may play a role in the long-term population dynamics of threatened and patchily distributed species, such as Dupont's Lark (Frederiksen *et al.* 2008).

In this study we have described the drastic population decline of Dupont's Lark after an extreme cold event. Due to the low number of studies assessing how extreme climatic events can impact bird populations and the expected increase in frequency and severity of extreme weather events over the following decades due to climate change, our findings are useful to improve understanding of the impacts of extreme cold events on the population dynamics of birds. Our results may also be useful for future studies with the species (or similar ones) aimed at understanding the impact of stochastic events on population dynamics (e.g. population viability analyses, climate change projections). Further studies may assess the impact of extreme weather events on both adult and juvenile survival and on subsequent reproductive success (Järvistö *et al.* 2016), to gain a more comprehensive view of the role that catastrophic events can have on long-term population dynamics.

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