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ORIGINAL ARTICLE

Effects of an extreme weather event over reproduction and survival of Great Tits (*Parus major*) in eastern Spain

Iris Solís[1] · **Elena Álvarez**[1] · **Emilio Barba**[1]

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Abstract
The frequency of extreme climatic and weather events has increased since 1950 due to global changes induced by human influence. These events can have significant impacts at the individual, population, and community levels across various taxonomic groups. They can be particularly detrimental to bird populations during their breeding season, affecting specific breeding parameters. This study originated from an exceptionally rare breeding season of a resident Great Tit population recorded in spring 2002 when an unusual mortality of nestlings was observed. We quantified weather conditions (temperature, rainfall) from the end of April, a few days before we started detecting failed nests, and compared them with previous and subsequent years. In early May, when many pairs were incubating or caring for newly hatched chicks, we detected unusually low ambient temperatures and unusually high rainfall. This event likely caused that many first clutches failed completely, and that, compared with previous and subsequent years, fledging and breeding success was relatively low in those which were successful. There was also an increased proportion of replacement clutches that year. Anyway, the overall production of fledglings per breeding pair over the breeding season was 2.39, lower than other years. Although recruitment rate in 2003 was similar to other years, the lower production of fledglings in 2002 probably resulted in a decrease in the number of breeding pairs in the following years.

Keywords Breeding success · EWE · Precipitations · Recruitment · Temperature

Zusammenfassung
Effekte eines extremen Wetterereignisses auf Reproduktion und Überleben von Kohlmeisen *(Parus major)* in Ostspanien

Die Frequenz extremer klimatischer und wetterbedingter Ereignisse hat seit 1950 aufgrund globaler Veränderungen, die durch anthropogene Einflüsse verursacht wurden, zugenommen. Diese Ereignisse können signifikante Auswirkungen auf individueller, populations- und gemeinschaftlicher Ebene bei verschiedenen taxonomischen Gruppen haben. Sie können besonders schädlich für Vogelpopulationen während ihrer Brutzeit sein und spezifische Brutparameter beeinflussen. Die vorliegende Studie geht auf eine außergewöhnlich seltene Brutsaison einer heimischen Kohlmeisenpopulation im Frühjahr 2002 zurück, als eine ungewöhnliche Sterblichkeit von Nestlingen beobachtet wurde. Wir quantifizierten ab Ende April die vorliegenden Wetterbedingungen (Temperatur, Niederschlag). Einige Tage zuvor begannen wir, erfolglose Brutversuche vorzufinden und verglichen diese mit den vergangenen und folgenden Jahren. Anfang Mai stellten wir ungewöhnlich niedrige Umgebungstemperaturen und hohe Niederschlagsmengen fest, zu einer Zeit, in der viele Paare am Brüten waren oder sich um die neugeborenen Küken kümmerten. Diese Ereignisse führten vermutlich dazu, dass viele Erstgelege vollständig scheiterten. Gelang die Brut dennoch, waren das Flüggewerden der Jungvögel und der Bruterfolg im Vergleich zu den Vorjahren und den

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✉ Iris Solís
soheri@alumni.uv.es

[1] Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia. C/ Catedrático José, Beltrán 2, 46980 Paterna, Spain

Folgejahren gering. In demselben Jahr gab es einen erhöhten Anteil an Ersatzgelegen. Dennoch betrug die Gesamtanzahl von Jungvögeln pro Brutpaar, welche flügge wurden, 2.39 Jungvögel. Im Vergleich zu anderen Jahren ist die Anzahl dieses Jahres niedrig. Obwohl die Rekrutierungsrate im Jahr 2003 ähnlich war wie in anderen Jahren, führte die geringere Zeugung von Jungvögeln im Jahr 2002 wahrscheinlich zu einem Rückgang der Anzahl von Brutpaaren in den folgenden Jahren.

Introduction

According to the latest reports from the Intergovernmental Panel on Climate Change (IPCC), global changes induced by human influence have likely increased the likelihood of currently rare extreme climatic events (ECEs, hereafter) since the 1950s (Seneviratne et al. 2021). Some examples of these events include the increased frequency and duration of heatwaves and droughts on a global scale, the growing intensity of heavy precipitation events and floods in the Northern Hemisphere, and the extended fire seasons in Australia and the United States (IPCC 2022). It seems that the increase in frequency and intensity of these extreme events will occur earlier than predicted (Suárez-Gutiérrez et al. 2023). In one of the IPCC's recent reports (2022), researchers assert that, due to the rise in global temperatures, there will be an increasing occurrence of some ECEs in the near future. They also distinguish between ECEs and extreme weather events (EWEs, hereafter): while EWEs are isolated events that are rare at a particular place and time of the year, ECEs refer to patterns of EWEs that persist for some time, such as a season (a few months) or longer (e.g., high temperatures, droughts, or total rainfalls over a season) (IPCC 2019).

Although widely used, the definitions of ECEs and EWEs are not clear, involve arbitrary cutoffs and none of those proposed is universally accepted (Bailey and van de Pol 2016). Smith (2011) proposed not to rely only on meteorological variables to define an EWE, but also to consider its ecological effects. In her words "an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability". Though Smith (2011) used the term "ECE", we will use EWE hereafter for the reasons outlined above.

Interest in EWEs among biologists has increased over the last few decades due to the increasing frequency of these events (Maxwell et al. 2018) and their potential extreme impacts at the individual, population, and community levels of many different taxonomic groups (e.g., Parmesan et al. 2000; van de Pol et al. 2010; Hoover et al. 2014; Tobolka et al. 2015; Gardner et al. 2017; Maxwell et al. 2018; Glądalski et al. 2020). The main challenge in studying the effects of these extreme events is their unpredictability; they must occur during ongoing studies, making it a matter of chance which species and biologically meaningful parameters are recorded. Nevertheless, it has been clearly shown that extreme weather events occurring during the breeding season can be particularly detrimental to bird populations, with reported specific effects on various breeding parameters. For example, they may result in laying (Martin and Wiebe 2004) or hatching delays (Glądalski et al. 2020), a reduction in chick survival and body condition (Dawson and Bortolotti 2000), and even nest desertion (Decker and Conway 2009). Individual survival could be also directly affected. For example, Altwegg et al. (2006) demonstrated that harsh winters and snowstorms led to a reduction in the survival of barn owls (*Tyto alba*). Consequently, understanding the impacts of these EWEs on individuals, populations, and communities is a crucial goal in ecological and conservation research.

The present study originated from an exceptionally rare breeding season of a resident Great Tit (*Parus major*) population in eastern Spain, which was recorded in Spring 2002. During this year, an unusual mortality of nestlings was observed, potentially associated with a brief event of low temperatures and high precipitations occurring within the breeding season. If confirmed, we would then have a simultaneous occurrence of relatively extreme weather conditions and relatively extreme ecological responses. Therefore, our first objective was to evaluate how extreme (i.e., different from usual values in this study area and time of year) ambient temperatures, rainfall and Great Tit reproductive traits were. As a second target, we will investigate whether meteorological extremes (as potential causal factors) and life history trait extremes (as ecological responses) could be linked. We hypothesized that the observed reduction in breeding output was connected to this extreme weather event. We explicitly tested the following predictions: (1) mean ambient temperatures were lower, and precipitation was higher during the days of the presumed EWE than the long-term mean (11 years centered on 2002); (2) mean values of the breeding parameters mostly determined before the EWE were not affected (i.e., they were similar to previous and following years); (3) mean values of the breeding parameters mostly determined within or after the presumed EWE were worse than those in previous or following years; (4) particular nests affected by the EWE showed more negative effects if the EWE occurred in more sensitive phases (e.g., with young nestlings); and (5) if the EWE reduced the number of fledglings produced, the proportion of first-year breeders the year following the EWE will be low relative to other years.

Methods

Study area and general field methods

This study was conducted on a resident Great Tit population breeding in nestboxes in Sagunto, eastern Spain (39° 42′ N, 0° 15′ W, 30 m a.s.l.). The study area was situated within an extensive orange *Citrus sinensis* monoculture plantation. Breeding data from this location is available from 1986 to the present (e.g., Álvarez and Barba 2014a; Rodríguez and Barba 2016; Solís et al. 2021). The size of the study area has expanded over the years. For this study, we focused on a subarea of 150 ha, which has remained constant with the same number of nestboxes during the years considered here. Specifically, for this study centred around 2002, we selected breeding data from 2000 to 2004 and temperatures and precipitation data from 1997 to 2007.

Each year, wooden nestboxes were hung from branches of the orange trees by late February, and they were removed after the breeding season, typically by late July. Whenever possible, nestboxes were placed in the same tree each year. Each nestbox underwent at least weekly checks, with more frequent checks during specific nesting phases, to record basic breeding parameters (e.g., Álvarez and Barba 2014a; Rodríguez and Barba 2016; Solís et al. 2021). Regular monitoring of all nestboxes was concluded when no new nests appeared in two consecutive weeks after mid-June, ensuring that all breeding attempts occurring each season were confidently recorded.

All dates are presented as "April dates" (1 = 1st April), and the laying date of each clutch was calculated assuming that one egg was laid per day (Álvarez and Barba 2014a). The clutch was considered complete when no more eggs were laid during two consecutive days, and the female began full incubation. Following this, all the eggs from as many clutches as possible were measured for length and width during the period between clutch completion and hatching. The volume of each egg was estimated, and the mean volume was computed for each clutch (Barba et al. 1995).

When nestlings were 10–12 days, adults were captured with door-traps at the entrance of the nestboxes, and if not already ringed, they were fitted with individually numbered metal rings. The sex and age (first-year or older) of each individual were noted following Svensson (1992). Nestlings were also individually ringed at 15 days. Nestling tarsus length and body mass were recorded during ringing, and mean values for each brood were calculated.

We classified as first clutches those that started within the first 30 days after the initiation of the first clutch of that year, following the criteria of van Noordwijk et al. (1995), Visser et al. (2003), and Álvarez and Barba (2014a). The remaining clutches were categorized as either "second" (the second clutch after a successful one), "replacement" (the second clutch following the failure of the first one), or "unknown" (late clutches that could not be assigned to the previous categories) (refer to Solís et al. 2021 for detailed information).

We defined hatching success as the percentage of hatched eggs relative to the original clutch size, fledging success as the percentage of fledglings that left the nest in relation to the number of hatchlings, and breeding success as the percentage of fledglings that left the nest in relation to the number of eggs laid. In this context, we considered a clutch successful when at least one chick fledged from the nest and classified it as failed when none of the chicks managed to fledge.

Temperature and precipitation data and EWE definition

We utilized temperature and precipitation data recorded by the Spanish Meteorological Agency at the meteorological station "Sagunto-Pontazgo," located 4 km from the study area. For this study, we focused on minimum and maximum daily temperatures as well as daily precipitation during May for the period 1997–2007 (covering 5 years before and 5 years after our focal year). In 2002, there was a malfunction in the meteorological station, and temperatures from days 10 to 22 were not available. We estimated these missing data using the protocol outlined by Miró et al. (2015) and data from nearby stations. In short, the method is based on the statistical downscaling and spatial interpolation of high-resolution temperatures by using as many records as possible from nearby meteorological stations. The method was tested and validated using data from the 1948–2011 period performed for the Valencia Region (east Iberian Peninsula).

From these raw data, we computed May mean daily temperatures as the average of daily minimum and maximum temperatures, both for our study period (1997–2007) and for the specific year 2002. Regarding precipitations, we determined the total daily precipitation for the same month.

From these records, we first classified "extremely cold days" as those where the daily mean temperatures in 2002 were equal to or lower than the 10th percentile of the long-term (1997–2007) mean for each respective day. Second, we identified "days with extreme precipitations" as those where daily precipitation was equal to or exceeded the 90th percentile of the long-term total for each specific day. We will consider an EWE as several consecutive days with extremely cold temperatures and/or extreme precipitation.

Data analysis

To analyse the ecological consequences of this potential EWE, we sought significant differences in breeding parameters of first clutches (laying date, clutch size, mean egg volume, mean nestling body mass and tarsus length, and hatching, fledgling, and breeding success) between the focal study year and the preceding and succeeding years. For this study, we selected data from the period 2000 to 2004 (i.e., from 2 years before to 2 years after our focal year). We employed ANOVAs, followed by post hoc Tukey's HSD tests when significance was observed. Percentages (hatching, fledgling, and breeding success) underwent arcsin square root transformation for analyses (Zar 1996). As an estimation of local survival, we calculated the percentage of fledglings recaptured as breeding birds in our population any of the next 2 years after each breeding season.

We also examined the general recruitment of first-year birds into the breeding population. In normal conditions, we would expect the proportion of first-year breeders to be similar between years, with notable deviations occurring only in cases of exceptionally bad or good years. In this comparison, we distinguished between "local" first-year breeders (those fledged from nestboxes within our study area) and "immigrants" (first-year breeders coming from outside the study area). This distinction allows us to differentiate between local and regional effects. For example, if a negative event only impacted our local population within our study area, resulting in low fledging success, the proportion of first-year breeders in the next year could be similar to other years if more birds from outside (immigrants) join. On the other hand, if there were unfavourable breeding conditions at a regional scale, the proportion of first-year breeders would be low, with the proportions of local and immigrant birds being similar to other years.

All analyses were conducted with the IBM SPSS Statistics 25 software.

Results

May temperatures and precipitations

In general, the mean daily temperatures in 2002 (17.9 °C) were not significantly different from our long-term mean (1997–2007; 18.9 °C). However, during May 2 to May 8, 2002, the mean daily temperatures were notably low, with 5 out of these 7 days being equal to or lower than the 10th percentile of the study period (Fig. 1).

Regarding precipitations, May 2002 was wetter compared to the study period. From 1997 to 2007, the mean total precipitation in May was 14.29 mm, whereas in 2002, it was 45.32 mm. Between May 2 and May 8, we recorded a period of heavy rains, with daily precipitations on 4 out of these 7 days being equal to or higher than the 90th percentile of the study period (Fig. 1).

The period of cold temperatures coincided with the period of heavy rains (Fig. 1). We selected May 2 as the initial day of this period because of the sharp drop in temperature between days 1 and 2 (almost 5 °C), and the onset of precipitation on day 2. May 8 was the last day with rainfall and also the last relatively cold day. Therefore, based on these results, we concluded these 7 days (between May 2 and May 8) could be considered as a period of extreme weather in the study area, and we will refer to it as an EWE hereafter.

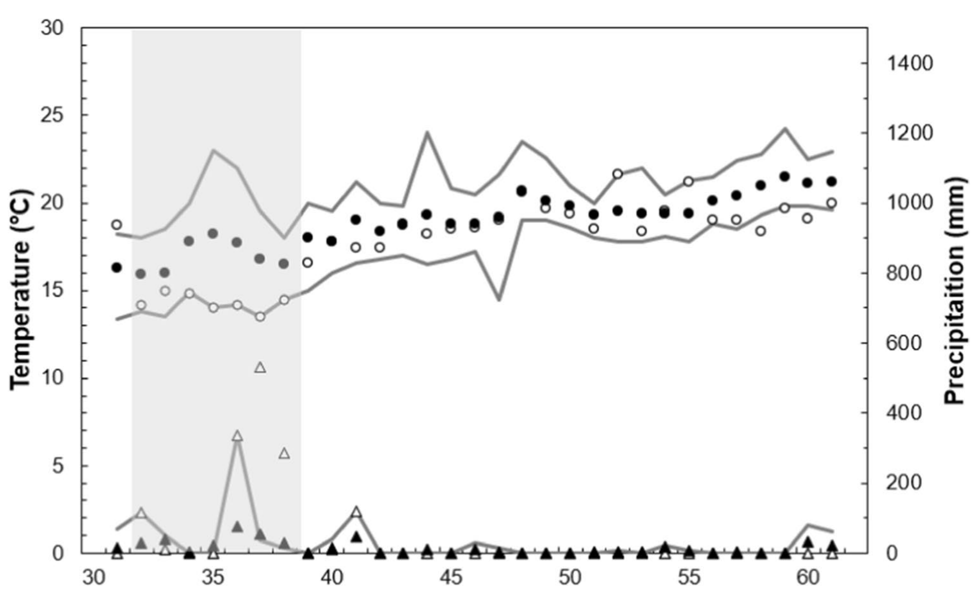

Fig. 1 May's mean temperatures and total daily precipitation from the study period. Dots depict mean temperatures, while triangles, daily precipitations (black for the study period -1997 to 2007- and white for 2002). The upper grey line depicts the 90th percentile for daily mean temperatures, while the middle one depicts the 10th percentile and the lower one depicts the 90th percentile for daily precipitations from the study period. The grey box points out the coincidence between the period of cold days and heavy rains. Dates at X-axis are presented as 'April dates' (i.e., 31 = May 1st)

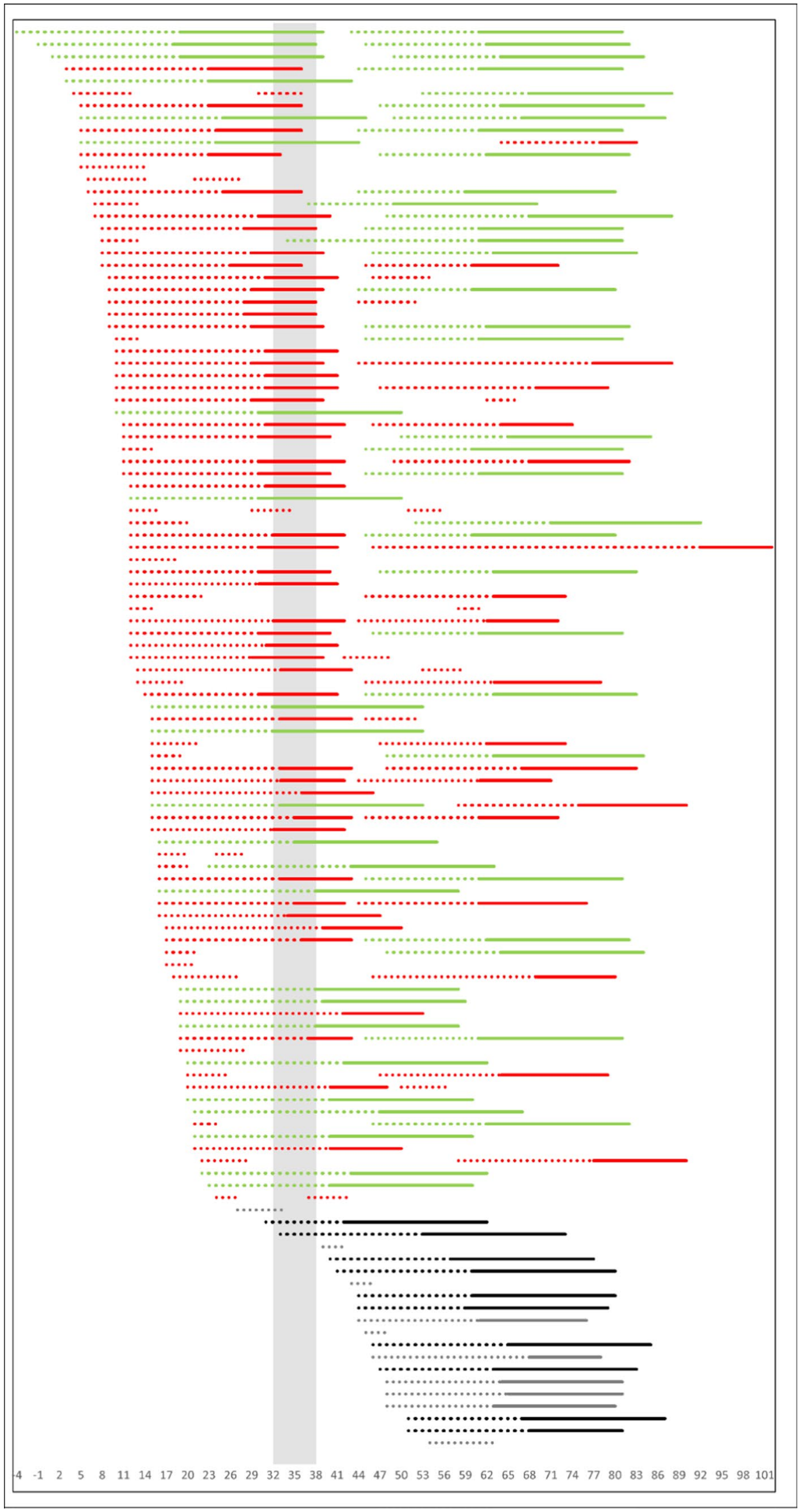

Fig. 2. Nests affected by the EWE in 2002. Each row drawn on the y-axis represents a different nest. Points depict the laying and incubation phases, while continuous lines illustrate the chicks' brooding phase. The colour green denotes successful nests where at least one fledgling leaves the nest, while the colour red signifies failed nests. Replacement clutches are observable when a red line is followed by another one, and second clutches are identified by following green lines. Grey lines designate unknown clutches (those that could not be classified as replacement or second clutches but could not be first ones either). The grey box indicates the occurrence of the EWE. Dates on the x-axis are presented as 'April dates' (i.e., 31 = May 1st)

Active nests during the EWE

Out of the 96 first clutches laid in 2002, 71 (73.96%) were active (with eggs or nestlings) during at least part of the 7 days encompassed by our defined EWE (Fig. 2). At the midpoint of this EWE (day 35), there were 21 nests (29.58% of the 71 active ones) in the incubation phase, 43 nests (60.56%) with young nestlings (10 days or less), and 7 nests (9.86%) with older nestlings (Fig. 3).

Breeding performance

The mean laying date of first clutches exhibited significant differences between the study years (2000–2004), with 2001 being the earliest and 2004 being the latest. The mean laying date in 2002, the year of the EWE, was significantly later than in 2001 but earlier than in 2004, showing no significant difference from either 2000 or 2003 (post-hoc Tukey tests; Table 1).

There were also between-year differences in the mean clutch size of first clutches. The smallest mean clutch size was recorded in 2001, and the largest in 2004. In 2002, the mean clutch size was significantly larger than in 2001, with no significant difference from any of the other 3 years (Tukey tests; Table 1).

Mean egg volume also exhibited significant differences between years, being the smallest in 2004 and the largest in 2000. In 2002, the mean egg volume was significantly smaller than in the two preceding years, while it did not differ from 2003 and 2004 (Tukey tests; Table 1).

Hatching success from first clutches differed significantly between years, being the smallest in 2001 and the highest in 2003. However, hatching success in 2002 did not differ significantly from any of the other 4 years (Tukey tests) (Table 1).

There were also significant between-year differences in fledging success, with 2002 having the lowest and 2000 having the highest success. The value for 2002 was significantly lower than those of all the other years (Tukey tests) (Table 1; Fig. 4). Regarding breeding success, between-year differences were found again, with 2002 having the smallest and 2000 having the highest breeding success. In 2002, breeding success was significantly lower than in 2000, 2001, and 2003 (Tukey tests) (Table 1).

No significant differences were found in mean nestling body mass between years (Table 1). Nestling mean tarsus length differed between years, being the shortest in 2002, but this value only differed significantly from that of 2000, which showed the longest value (Tukey tests; Table 1).

In relation with previous and later years, we also detected an increased proportion of complete failure among first clutches in 2002, which turned into an increased proportion of replacement clutches this year (Table 2). Among these failed first clutches, 45 of them (61%) had chicks with 10 days or less, 34% were in the laying or incubating phases, and 5% had nestlings older than 10 days.

Fledgling survival and population effects

In 2002, a total of 244 chicks successfully fledged from first, replacement, second, and unknown clutches of 98 breeding pairs, that is 2.39 fledglings per pair. The figures were 5.17 fledglings per pair in 2000, 3.92 in 2001, 5.06 in 2003 and 3.63 in 2004. Only 14 from these 244 fledglings in 2002 (6%) were recaptured as breeding birds in the population within the subsequent 2 years (2003 and 2004). The

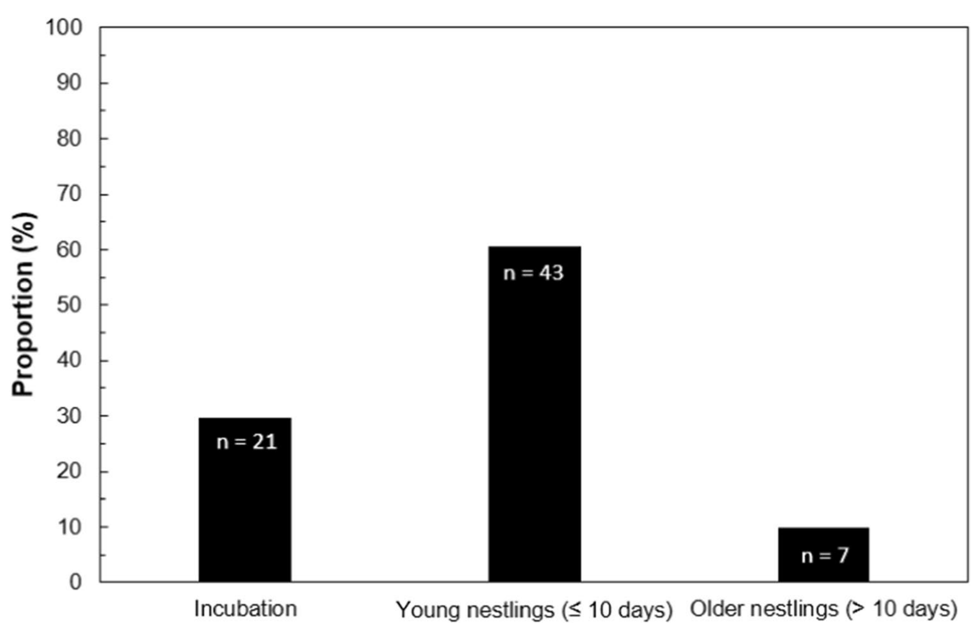

Fig. 3 Proportion of active nests from the first clutches at the middle of the EWE (day 35, April dates) and the phase at they were when this event occurred. Small nestlings make reference to those who are 10 days or less, while older nestlings are those who are more than 10 days old. Sample size = 71 nests

Table 1 Means of the different breeding parameters

Breeding parameter	2000	2001	2002	2003	2004	*F*	*P*
Mean laying date	11.59 (A) (SE = 5.78, *n* = 120)	**4.87 (B)** (SE = 5.84, *n* = 98)	12.67 (A,C) (SE = 5.60, *n* = 96)	14.23 (C) (SE = 7.20, *n* = 70)	**19.13 (D)** (SE = 5.55, *n* = 24)	43.660	<0.001
Clutch size	8.19 (A) (SE = 1.08, *n* = 113)	**7.25 (B)** (SE = 1.30, *n* = 95)	7.93 (A) (SE = 1.06, *n* = 83)	8.23 (A) (SE = 1.07, *n* = 65)	8.47 (A) (SE = 0.61, *n* = 19)	12.523	<0.001
Egg volume (mm^3)	**1519.32 (A)** (SE = 126.65, *n* = 96)	**1518.67 (A)** (SE = 116.04, *n* = 90)	1460.79 (B,C) (SE = 124.96, *n* = 80)	1513.70 (A,C) (SE = 137.27, *n* = 62)	1445.12 (A,C) (SE = 90.04, *n* = 21)	4.327	0.002
Hatching success (%)	73.67 (A) (SE = 36.48, *n* = 113)	65.74 (B) (SE = 39.87, *n* = 94)	71,97 (A,B) (SE = 35.88, *n* = 83)	80.95 (A,B) (SE = 28.65, *n* = 65)	68.84 (A,B) (SE = 40.46, *n* = 19)	2.865	0.023
Fledging success (%)	**79.84 (A)** (SE = 30.93, *n* = 101)	**65.30 (A)** (SE = 39.56, *n* = 73)	20.92 (B) (SE = 34.41, *n* = 71)	**72.71 (A)** (SE = 39.56, *n* = 61)	**57.22 (A)** (SE = 40.63, *n* = 17)	31.218	<0.001
Breeding success (%)	**64.19 (A)** (SE = 37.18, *n* = 113)	**44.21 (B)** (SE = 40.79, *n* = 95)	13.60 (C) (SE = 26.33, *n* = 83)	**58.87 (A,B)** (SE = 39.22, *n* = 65)	38.10 (B,C) (SE = 36.04, *n* = 19)	25.96	<0.001
Nestling body mass (g)	17.08 (A) (SE = 1.42, *n* = 91)	16.90 (A) (SE = 1.26, *n* = 58)	17.06 (A) (SE = 1.27, *n* = 22)	17.09 (A) (SE = 1.38, *n* = 50)	16.50 (A) (SE = 1.50, *n* = 14)	0.687	0.602
Nestling tarsus length (mm)	**19.47 (A)** (SE = 0.58 *n* = 90)	19.09 (B) (SE = 0.76, *n* = 58)	19.01 (B) (SE = 0.92, *n* = 22)	19.36 (B) (SE = 0.49, *n* = 49)	19.16 (B) (SE = 0.22, *n* = 14)	4.616	0.001

Differences between years were tested using Oneway ANOVAs. Hatching, fledging, and breeding success were arcsin square root transformed for the analyses, but we present here the percentages for an easier visualisation. Letters following each value indicate the results of the post-hoc analyses, being means with different letters statistically different. Bold values indicate differences statistically significant in relation to 2002. Standard errors and sample size for each variable and each year are presented between brackets

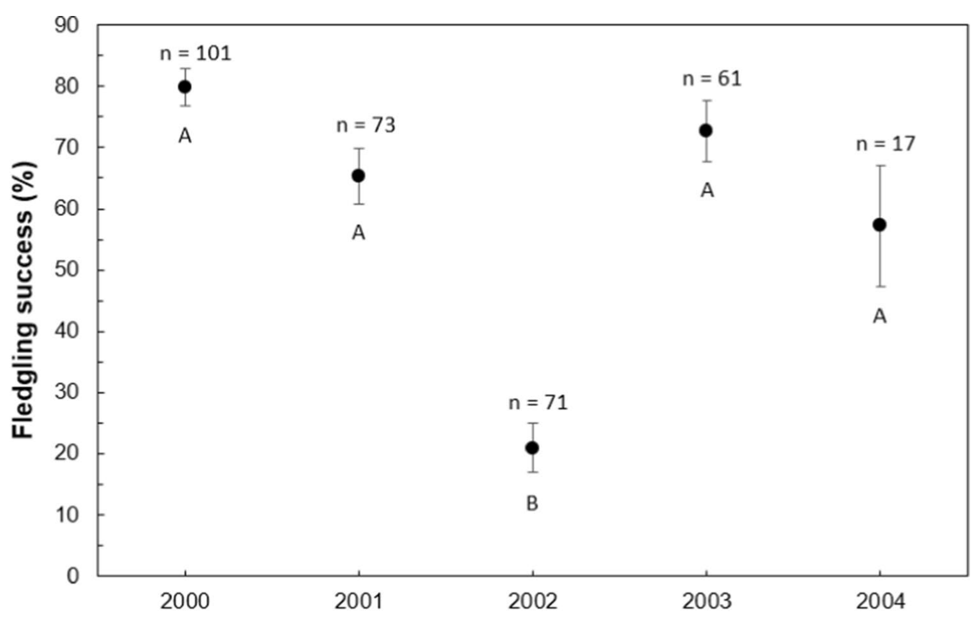

Fig. 4 Fledging success proportion in each year of the study period. Dots represent mean fledging success for each year, while the bars represent their standard deviation. Letters below the bars show differences between groups according to Tukey's HSD tests. Sample size = 323 pairs

Table 2 Number of breeding pairs (NBP), proportion of failed clutches from first ones (FC) and proportion of pairs laying a first and a replacement clutch (FRC)

Years	NBP	FC (%)	FRC (%)
2000	122	24.59	11.48
2001	98	40.82	28.57
2002	98	77.55	62.24
2003	72	29.17	6.94
2004	25	44.00	0.00

Table 3 Number of breeding individuals (NBI) captured each year (i.e., number of individuals identified by its metallic rings in either clutch type, while they were breeding), percentage of first-year individuals (FY) among captured individual each year and, within these, percentage of first year immigrant (II) and of first year local individuals (LI)

Years	NBI	FY (%)	II (%)	LI (%)
2000	194	27.32	71.70	28.30
2001	159	36.48	62.07	37.93
2002	139	38.85	61.11	38.89
2003	126	11.90	60.00	40.00
2004	42	21.43	33.33	66.67

corresponding figures were 4.8% in 2000, 9.4% in 2001, 2.6% in 2003, and 5.5% in 2004. Therefore, local survival in 2002 was within the range of preceding and subsequent years.

Notably, none of the 11 chicks originating from nests affected by the EWE during the egg-laying phase were recaptured in the next 2 years. Among the 47 chicks from nests impacted by the EWE during the incubation phase, 6 were recaptured (12.76%). From the 26 chicks from nests affected by the EWE when nestlings were 10 days or less, 4 were recaptured (15.38%). Finally, none of the 23 chicks from nests affected by the EWE when nestlings were older than 10 days were recaptured. On the other hand, 146 chicks fledged from nests not affected by the EWE at any stage, and only 4 of them (2.74%) were recaptured within the next 2 years.

The proportion of first-year breeders among our breeding population in 2000 and 2001 was around 30% (Table 3). Even in 2002, the year when the studied EWE occurred, 39% of the breeding individuals were first-year breeders. In sharp contrast, the proportion of first-year breeders dropped to only 12% in 2003 and it was also relatively low in 2004 (21%). Moreover, the proportion of local and immigrant first-year breeders was similar (29–40% locals, 60–72% immigrants) in 2000, 2001, 2002 and 2003. It is remarkable how these figures inverted in 2004, where 67% were locals and only 33% were immigrants.

Overall, the number of breeding pairs decreased dramatically from 2000 to 2004, with a very sharp decline between 2003 and 2004 (Table 2).

Discussion

Extreme weather event

Based on the temporal coincidence of several consecutive days with extremely cold temperatures and heavy precipitations between May 2 and May 8, 2002, we designated this period as an EWE. The lowest mean daily temperature and the highest daily precipitation recorded during this week were 13.5 °C and 530 mm, respectively. Both extremes occurred on May 7.

Before the EWE: laying date, clutch size and egg volume

The laying date and clutch size in Great Tits are primarily influenced by prey availability and temperatures preceding the initiation of the clutch (Perrins and McCleery 1989). The occurrence of an EWE with cold temperatures or snow during the early phases of breeding could result in a delay in mean laying dates (e.g., Martin and Wiebe 2004; Glądalski et al. 2014). The only study we are aware of relating extreme weather (heavy rainfall, extreme hot or cold days) on clutch size (Marrot et al. 2017) did not find any significant effect, even using a more demanding threshold to define the extreme weather event (5% percentiles).

On the other hand, egg volume is determined during the laying period. Many studies have identified multiple factors that could affect egg volume, including the body and physiological condition of females, territory quality, prey abundance, and environmental conditions (Bańbura et al. 2010; Bańbura et al. 2018; Golawski and Mitrus 2018). However, none of the previous studies seem to have investigated the effect of an EWE on the volume of the eggs laid.

The EWE detected in 2002 occurred after the completion of all the first clutches that did not fail (due to abandonment or predation) before completion. Consequently, we would not anticipate that either the mean laying date, mean clutch size, or mean egg volume would have been affected by the adverse environmental conditions during this period. Accordingly, all three parameters varied between years, but their values for 2002 were not notably worse compared to previous or subsequent years. This aligns with our hypothesis that the breeding parameters determined before the EWE were, in general, within the range of values observed in previous and later years.

Effects of the EWE on hatching success and nestling growth

Incubation is energetically costly, and this cost may vary depending on environmental and individual characteristics (Reid et al. 2002). Females must avoid the freezing or overheating of the eggs, as an abrupt change in ambient conditions during incubation may impact the development of the embryos and, consequently, breeding success (Deeming 2002). The complex relationship between temperature and incubation behaviour may co-vary and interact with other constraints, such as female body condition. Weather conditions may alter a female's incubation behaviour, and adverse weather conditions, such as cold temperatures and precipitation, might compel females to shorten incubation sessions and recesses and to take shorter off-bouts searching for food for self-maintenance. This is because they need more energy to cope with cold temperatures and because insects would be more challenging to find under these unsuitable conditions (Frampton et al. 2000; Arlettaz et al. 2010; Coe et al. 2015; Marasco and Spencer 2015). Females have some ability to withstand low ambient temperatures, avoiding negative effects on the embryos (Álvarez and Barba 2014b, Vaugoyeau et al. 2017). However, prolonged absences from the nest could still impact embryo survival and, consequently, lower hatching chances. In 2002, hatching success in our studied Great Tit population did not differ from any of the other 4 years. Thus, females affected by the EWE during the incubation phase were able to compensate for these adverse weather conditions, avoiding passing the costs onto their eggs.

After hatching, several studies have shown that, during heavy rainfall and lower environmental temperatures, females tend to stay longer in the nest, particularly during the first 7 days of the nestling phase. Consequently, they decrease their feeding rates to spend more time brooding (Radford et al. 2001; Deeming 2002; Álvarez and Barba 2014b). Younger nestlings are more susceptible to fluctuations in temperatures and precipitations, possibly due to their inability to thermoregulate, given their underdeveloped feathers. They depend on the heat provided by the female during this period. Additionally, chicks may not be fed adequately, or they may still have high food demands despite frequent brooding (Marques-Santos and Dingemanse 2020). As adverse weather conditions negatively affect the provisioning rate (especially during cold and rainy days), chick survival would be compromised and, consequently, reproductive performance would be negatively affected (Dawson and Bortolotti 2000; Arlettaz et al. 2010; Tobolka et al. 2015). Similarly, extreme conditions may lead to a reduction in prey availability, particularly critical for insectivorous birds like Great Tits during their breeding season (van Noordwijk et al. 1995; Wilkin et al. 2009; Arlettaz et al. 2010). Collectively, these circumstances may diminish the available energy for the proper development and growth of the chicks (Öberg et al. 2015). However, we did not observe a significant effect on nestling body mass (no differences compared to other years) and tarsus length (only smaller in 2002 than in 2000). This means that those nestlings that managed to survive to fledge achieved standard fledging conditions for the population despite the EWE. Nevertheless, it should be noted that only 21% of the hatchlings survived to fledge—this means that most nestlings died into the nests.

Effects of the EWE on breeding success

Although they do not refer to extreme events, many studies have checked that unfavourable ambient conditions during the breeding season are related to a higher clutch failure and a lower production of chicks (Eeva et al. 2002; Rodríguez and Bustamante 2003; Arlettaz et al. 2010; Öberg et al. 2015). Both, the study by Arlettaz et al. (2010) with Hoopoes (*Upupa epops*) and the one by Öberg et al. (2015) with Northern Wheatears (*Oenanthe oenanthe*) showed that heavy rainfalls and/or low temperatures during the nestling period affected negatively nestling survival.

Accordingly, we observed both effects on our population with the occurrence of an EWE. First, there was a relatively high proportion of nests that failed completely, most of them with chicks aged 10 days or less. This, in turn, resulted in a very high proportion of pairs laying replacement clutches in 2002. Second, the proportion of chicks successfully fledging was relatively lower than in previous and subsequent years. Our study population breeds in eastern Spain, about 4 km away from the Mediterranean Sea. Temperatures are generally mild during the breeding season (e.g., mean temperatures around 16 °C in April (Solís et al. 2023)). Weather episodes as extreme as the one reported here have not occurred since 1986, when the long-term study of this population was started, until now (2024). It is therefore likely that our population is not accustomed to facing extreme and unpredictable ambient conditions like the one occurred in 2002, and it could be more vulnerable to this kind of events (e.g., Eeva et al. 2002). Our results indicate that parental care was insufficient to guarantee nestling survival, probably due to higher heat and food requirements under these climatic conditions, especially for the youngest chicks.

Years after the EWE

Summarizing the negative effects on breeding performance, 2002 was characterized by a high number of failed nests and a low production of fledglings from those successful nests. Although many more replacement clutches than usual were laid by pairs whose first one failed, breeding success of these late clutches is typically low. Then, the overall effect was a relatively low number of fledglings produced per breeding pair compared with the rest of the years. Post-fledgling survival, estimated as the percentage of fledglings recruited into the breeding population the next 2 years, was not out of the range of previous and subsequent years. Thus, we concluded that environmental conditions outside the breeding season did not seem to have been abnormally stressful for them. Although population consequences of EWEs are intrinsically difficult to study, at least a couple of studies have tried to do so, both concerned with catastrophic floods. Thus, van de Pol et al. (2010) showed that catastrophic floods reduced the reproductive output below stable population levels in Eurasian Oystercatchers (*Haematopus ostralegus*). On the other hand, Tryjanowski et al. (2009) also documented that an extreme flooding event in 1997 caused a massive loss of White Stork (*Ciconia ciconia*) chicks in Central and Eastern Europe that year, although long-term effects on population size were virtually null. We have not found, however, studies relating cold or hot spells on avian population dynamics. In our case, the low number of fledglings produced in 2002 had a clear impact on the size of the breeding population next year. We showed that this was, at least, a regional effect, since the proportion of first year local and immigrant individuals was similar than in other years, meaning that the low numbers of recruits was not specific of our studied nestbox population.

Conclusion

Considering both meteorological (temperature, precipitation) and ecological variables (Great Tit breeding performance and population size), we can conclude that a period of extreme weather conditions occurred in Sagunto during the first days of May 2002. By following the phenology of events, including how and when nest losses occurred, we provide convincing evidence for a causal relationship between bad weather and breeding failure. Great TitThis translated into a dramatic population decline in the following 2 years.

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Data availability The datasets generated during and/or analysed during the current study are available from the correspondingauthor on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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