**A spring cold snap is followed by an extreme
reproductive failure event in a mountain
population of pied flycatchers *Ficedula
hypoleuca***

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24 **Capsule** Very low and anomalous temperatures in early spring of 2010 were followed
25 by the only massive reproductive failure event recorded in 24 years in a population of
26 pied flycatchers *Ficedula hypoleuca* breeding at 1200 m altitude at Valsaín, central
27 Spain.

28 **Aim** To estimate the effects of an extreme climatic event on reproductive success in a
29 montane population of a long-distance migratory bird.

30 **Methods** To compare nestling growth and mortality in nests of different brood sizes in
31 the context of a brood manipulation experiment.

32 **Results** Total failure affected 36% of the broods and only 2.5 nestlings on average
33 were raised to fledging age. Most mortality affected broods in the second week of
34 nestling life. Fledglings attained very low values for mass and wing length compared
35 with long-term averages. Subsequent local recruitment was the lowest for any cohort in
36 24 years. The typical date-dependent decrease in breeding success in the population
37 was inverted.

38 **Conclusion** Breeding success was markedly affected by a weather event happening
39 one month before hatching and lasting only a few days. An increased frequency of
40 extreme weather events as predicted by some climate change scenarios may
41 dramatically affect insectivorous avian populations in the future.

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Climate change has been predicted to lead to higher rates of extreme climatic events (Rind *et al.* 1989, Liang *et al.* 1995, Easterling *et al.* 2000). Thus, cyclones (King *et al.* 1992), droughts (Fletcher & Koford 2004), heat waves (Salzman 1982) and cold springs (Wiggins *et al.* 1994) have been reported as inducing mass reproductive failure in birds (reviewed in Moreno & Møller 2011). The literature on adaptation to climate change primarily involves research into effects of climate trends, not extreme events (Jentsch *et al.* 2007). Incorporating responses to extreme events may give a more balanced view on the potential impacts of climate on populations. Thus, extreme weather conditions may have stronger effects on population dynamics than average climate (Knopf & Sedgwick 1987, Franklin *et al.* 1992, Hellman 2002, Saunders *et al.* 2011). Animal populations may suffer important set-backs after extreme climatic events for which recovery time may exceed intervals between such events if their frequency increases in a climate change scenario.

The winter of 2009/2010 was extreme throughout the northern hemisphere (Wang *et al.* 2010). The record-breaking cold temperatures from North America to Europe and Asia that winter were linked with extremely negative values of the North Atlantic Oscillation (NAO) index. Low NAO values in winter are normally associated with warm and humid conditions in Southwest Europe. Although the months of January-March 2010 were extremely wet in Spain as expected from low NAO values, this normal precipitation pattern was accompanied by very low temperatures in central and northern Spain during January-March (Spanish Meteorological Agency AEMET, annual reports). In marked contrast, April temperatures were 2 °C higher than normal. In the first days of May, a cold snap in central Spain led to record-breaking low temperatures directly following mild conditions (Spanish Meteorological Agency AEMET, annual reports). Freezing temperatures especially affected mountain areas.

While plant phenology was delayed by 10-15 days in central Spain at the beginning of April 2010, this consequence of the previous harsh winter conditions had

been erased by the end of the month (AEMET, phenology reports). Oak buds start to open in the first days of May in the pied-de-mont forests of the central Spanish mountain system as is usual following mild April temperatures (Sanz *et al.* 2003). The dramatic cold snap in the first days of May implied that minima reached freezing over large areas (AEMET annual report), a long-term record for that time of year. Own observations at 1200 m above sea level (asl) showed that buds of early-budding oaks were instantly killed by the cold snap while their opening was abruptly stopped in other trees. Moreover, oak budding was considerably delayed at higher altitudes. Here we show that these anomalous spring conditions were followed by the only mass reproductive failure recorded in 24 years (1991-2015) of research on a mountain population of Iberian pied flycatchers *Ficedula hypoleuca iberiae*. A brood manipulation experiment planned for a year without mass failure was conducted in 2010 and associated with detailed nestling mortality checks at the nests. What was to be a manipulative experiment on brood size was conducted in what became an anomalous year and the results thus provided insight into the effects of sudden climatic extremes on breeding success of an insectivorous passerine.

METHODS

General methods

Since 1991 we have studied a population of Iberian pied flycatchers breeding in nest-boxes in a montane oak (*Quercus pyrenaica*) forest at 1200 m.asl in Valsaín, Segovia, central Spain (40° 54'N, 04° 01'W) (see Sanz *et al.* 2003 for a description of the study area and population). All nest-boxes (approximately 300) are repeatedly inspected each spring and occupation by pied flycatchers recorded (50-125 are occupied by Iberian pied flycatchers). We have collected breeding data from all pied flycatcher nests between 1991 and 2014 by visiting the nest-boxes every 2-3 days from early May

(birds arrive during the second half of April) to end of June. The mean clutch size in the population is 5.60 ± 0.04 ($n=24$ years) and the mean brood size is 4.64 ± 0.08 (24 years) nestlings. Nestlings fledge with 16 days and cannot be handled after day 13 without inducing premature fledging. Hatching date is obtained through daily inspections when full clutches have been incubated for 12 days (duration of incubation is 13-15 days). The first observation of a nestling is then established as hatching date. We have thus obtained information on laying date, hatching date and the number of nestlings alive at 13 days (hatching date = day 1). We have obtained the biometrical measurements of all nestlings when 13 days old. We have ringed adults and nestlings with numbered aluminium rings, measured their tarsus length with a digital calliper to the nearest 0.01 mm and weighed them with a Pesola® spring balance (precision of 0.25 g). Folded wing length has been measured since 2002 with a stopped ruler to the nearest mm. As we have conducted different field experiments on this population throughout the long-term study, only non-experimental nests have been included in long-term comparisons. Hatching success is calculated as the number of hatched eggs divided by clutch size. Fledging success is calculated as the number of fledged young divided by the number of hatched nestlings. The death of complete broods has been noted without confirmation if some parent was still provisioning the brood when the death of the last nestling occurred or if the brood had been deserted.

Local climatic information was provided by the Spanish Meteorological Agency (AEMET). The weather station (Segovia, station no. 2465, coordinates: 40° 56' 43" N, 4° 7' 35" O) is located 9 km from the study area and at the same altitude.

Brood manipulation

This experiment was conducted unawares of the impending dramatic conditions for the population which could not be detected before hatching of the young. The cold snap

(see below) happened before the beginning of egg-laying in the population (no laying occurs in the first week of May). Two days after hatching was detected during daily nest checks, two or one nestling were transferred between simultaneously hatched reduced broods (n=21) and enlarged broods (n=21). A control group of 30 nests with a similar distribution of hatching dates as in the other treatments was left unchanged with respect to brood size, although nestlings were handled at the same age. The number of nestlings transferred depended on brood size at hatching, with broods of 5 and 6 hatchlings losing or receiving two nestlings and broods of 4 losing or receiving one nestling (there was only one brood of 7 which was kept as control). Nests were visited at 3, 7, 9, 11 and 13 days of age to check for nestling mortality and stage of total failure.

Statistical analyses

Data on breeding success for 2010 were compared with data for control broods in the other years. Results from the brood manipulation experiment included all nests for 2010. Treatments have been compared with parametric or non-parametric tests depending on data distributions (Statistica package, STATSOFT). Medians are presented with quartiles for nonparametric distributions and as means with standard errors (SE) for normal distributions.

RESULTS

Climate

In 2010 minimum temperatures during the first week of May in the study area attained very low values including freezing conditions following directly after exceptionally warm weather in the last days of April (Fig. 1). The difference in minima between April 29 and

May 6 was 15°C (Fig. 1). On the other hand, mean daily minimum temperatures during June 2010 when broods were being raised were within the 95% confidence interval for other years.

Comparison of breeding success with other years

Hatching success (91.6 %) was close to the average for all years (90.3 ± 1.3 %, $n=23$ years). However, fledging success (53.8%) was the lowest for the whole study period and clearly lower than for other years (79.9 ± 1.7 %, range 66-93%, $n=23$ years). In total 26 or more than a third of broods suffered total mortality before the age of 13 days. Total mortality affected less than 12% of broods in other years (average 5.1 ± 0.7 %, range 0-11.2%). While on average 4.6 ± 0.1 (range 3.8-5.3, $n=23$ years) chicks per nest were raised in other years, only 2.7 ± 0.4 nestlings on average ($n=30$ control broods) fledged in 2010. Fledglings weighed 1 g less on average (12.6 ± 0.3 g, $n=18$ control broods with surviving nestlings at 13 days) than the average for other years (13.6 ± 0.1 g, range 11.9-14.8, $n=23$ years). They also showed the shortest mean tarsi (16.8 ± 0.1 mm, $n=18$ broods) recorded (17.39 ± 0.05 mm, range 16.98-17.85 mm, $n=23$ years). Mean wing length (41.4 ± 0.8 mm, $n=18$ broods) was also the shortest since 2002 (45.8 ± 0.4 mm, range 42.8-47.8, $n=12$ years).

Brood manipulation

Total failure affected 19% of reduced broods, 37% of control broods and 52% of enlarged broods. Frequencies of total failure differed significantly between reduced and enlarged broods ($\chi^2=5.08$, $p=0.024$), but not in other comparisons between treatments. There was no significant difference between treatments in the number of nestlings fledged in the three experimental treatments (Table 1).

There was barely any mortality in the nests before the age of 3 days (Table 1). Absolute mortality (no. of dead chicks) was detectable in control and enlarged broods in the periods 3-7 and 9-11 days and only for enlarged broods in the period 7-9 days (Table 1). However, absolute mortality did not differ between treatments for any period (Table 1). Mortality rate (%) during the first week after hatching was detectable for control and enlarged broods but did not differ between treatments (Table 1). However, mortality rate during the second week was significantly related to treatment (Table 1), with a significant difference between reduced and enlarged broods ($H_{42}=7.2$, $p=0.014$). Total mortality rate increased from reduced to enlarged broods ($H_{42}=9.1$, $p=0.002$), and the median for enlarged broods was total failure (Table 1). More than half of mortality happened in the second week of nestling life and the proportions according to period (1-7 and 7-13 days) did not differ among treatments (Kruskal-Wallis $H_{48}=0.90$, $p=0.6382$).

Mass and wing length were significantly affected by treatment, with both measures declining with experimental brood size (Table 1). Nestlings in reduced broods had higher masses than nestlings in other treatments (Post-hoc Fisher LSD tests: reduced-control $p=0.005$, reduced enlarged $p=0.002$). Nestlings in enlarged broods had shorter wings than nestlings in other treatments (Post-hoc Fisher LSD tests: enlarged-control $p=0.032$, enlarged-reduced $p=0.004$). Only in reduced broods did nestlings attain masses before fledging which can be considered normal (Table 1).

Strikingly, the number of fledglings raised was positively (Fig. 2a) and second-week mortality negatively related to hatching date for all broods (Fig. 2b). Total failures were more frequent at early nests (Fig. 2). If only considering control broods, the trend was only significant for second-week mortality (Kendall $\tau_{29}=-0.43$, $p<0.01$).

Only 6 fledglings from the 2010 cohort recruited to the population, the lowest number for any year in the study period except 1996 when a mass predation event

occurred. This amounted to 3.3% of fledged young which is half the average recruitment rate for the rest of the study years ($6.7 \pm 0.01\%$, $n=21$).

DISCUSSION

The cold snap at the beginning of May 2010 in central Spain following mild April conditions was associated with dramatic reproductive failure in a population of Iberian pied flycatchers, the only such event witnessed by researchers in the study population in 24 years. The event was characterized by frequent total failures during the second week of life of nestlings, especially between the ages of 9 and 11 days. Moreover, fledged nestlings in non-deserted broods attained very low values for all measurements, especially for mass. There are several lines of evidence linking the event to conditions of extremely low food availability for nestlings and parents. First, broods were massively deserted in the second week of life, especially after the age of 9 days, when food demand by broods reaches its peak. Second, only experimentally reduced broods suffered normal levels of mortality and of nestling growth. Third, mortality and total failures hit strongest the early broods which are usually the more successful in the population, an inverted trend which may be linked to low caterpillar availability in the habitat. This leads to the inference that the cold snap with freezing temperatures in the morning during the period when oak buds normally open and folivorous caterpillars start their development, probably killed off the main prey base on which pied flycatchers depend for breeding (Moreno *et al.* 1995). Evidence for areas at higher altitudes (J. Moreno, unpubl. observations), where oaks show a later phenology, indicate that our study population occupied habitats critically affected by the May 2010 cold snap in the Spanish central mountain range.

Cold spells during the nestling stage have been shown to affect nestling mortality and growth in northern pied flycatcher populations (e.g. Virolainen 1984, Eeva

et al. 2002). In our study, the anomalous weather conditions during late April and early May were followed one month later by frequent total failure, high partial mortality and exceptionally poor nestling growth. Moreover, the weather conditions prevailing during the nestling stage of most broods were not exceptional and could not explain mass reproductive failure in our population. Thus we show that weather conditions of short duration can affect food availability one month later. The most plausible explanation for such delayed effects is that folivorous caterpillars failed to develop due to shortage of young leaves to feed on or to effects on reproducing adult moths. Folivorous caterpillars constitute the main prey base of pied flycatchers in the study area (Moreno *et al.* 1995). Freezing temperatures in early May may have completely stopped bud development in montane oak forests at altitudes where it had already started like our study area.

The frequency of total failures and nestling mortality were very low before the nestling age of 3 days, increased slightly to the age of 7 days and accelerated just as food demands by nestlings in connection with growth spurts reach their maxima (Lundberg & Alatalo 1992). Total failures were especially frequent between the ages of 9 and 11 days. Almost half of the total failures occurring at this stage affected enlarged broods, although not even reduced broods were immune to total failure. Individual nestlings also died with high frequency at this stage, reducing many broods at fledging to only 2 or 3 nestlings. The dramatic effect of brood enlargement on reproductive success is evidence of the cliff-edge effect postulated for clutch size limitation in stochastic environments (Boyce & Perrins 1987, Roff 2002). Clearly, large clutches are heavily penalized in extreme conditions in our population. Moreover, the apparent inability of females to predict future conditions at laying, which occurred after the cold snap, indicates that food availability for nestlings is not predictable several weeks in advance. The study indicates also that there are no efficient brood reduction mechanisms that can avoid total failure in our and possibly other populations. Our

experiment unintendedly showed that only in reduced broods did fledglings approach normal values for fledging mass. However, the food situation must have been so critical that even reduced broods suffered total failure. There were very few local recruits to the population from the 2010 cohort, suggesting that postfledging survival was extremely low for chicks raised during the mass failure event. Mean failure rate during normal conditions according to a revision of 14 studies on mass reproductive failures (Moreno & Møller 2011) was 27% but 79% during extreme conditions. Our failure rate of 36% is intermediate but is still extreme considering that it is more than twice as high as in other years. It is also higher than the 23% total failure rate in a Scandinavian population of the collared flycatcher *Ficedula albicollis* elicited by a cold spring (Wiggins *et al.* 1994). Breeding failure may have been linked to decreased adult survival (Moreno & Møller 2011). Unfortunately many adult birds suffered total failure before they could be caught, so we cannot estimate this effect accurately.

Early breeders in the population are those normally better adjusting the nestling stage to high availability of caterpillars and attaining a high reproductive success (Morales *et al.* 2007, Moreno *et al.* 2009, Ruiz-de-Castañeda *et al.* 2009). Late breeders provision may provision nestlings with increasing amounts of prey other than caterpillars (J. Moreno, unpubl. data), which are inadequate prey for growing nestlings of forest passerines (Banbura *et al.* 1999, Wilkin *et al.* 2009). In 2010, the typical date-dependent decrease in breeding success was inverted. It was early breeders that suffered the heaviest casualties, presumably because the caterpillar food base failed almost completely while alternative prey were still not available. Inverted date-dependent trends in breeding success may constitute a critical indication of food base failure for breeding insectivorous birds.

Published information on mass breeding failures in passerines is scant as most studies deal with seabirds and waders (e.g. Ganter & Boyd 2000, Gaston *et al.* 2002, Viera *et al.* 2006, Yannic *et al.* 2014). However, some studies on forest birds report

massive breeding failure linked to long-term drought conditions (Mac Nally *et al.* 2009). We conclude that the mass reproductive failure event detected in 2010 in our population may be a frequent undetected consequence of late cold snaps in Mediterranean mountain habitats as only long-term population studies may be able to register such events. Other populations of the species breeding at higher altitudes were not equally affected by the cold snap (J. Moreno, pers. obs.), indicating that local variation in vegetation and insect phenology may be paramount to explain the geographical distribution of such effects. In any case, an increased frequency of extreme weather events as predicted by some climate change scenarios (Moreno & Møller 2011) may dramatically affect insectivorous avian populations in the future. Increased future frequencies of early spring cold snaps as predicted by some climate change scenarios may have serious repercussions for birds in mountain habitats which depend on folivorous caterpillars.

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Table 1. Comparisons between experimental treatments in mortality and reproductive success variables (median and quartiles or mean $\pm$ SE) with non-parametric (Kruskal-Wallis, H) or parametric tests (ANOVA, F)

	Reduced (n=21)	Control (n=30)	Enlarged (n=21)	Test
Brood size after manipulation	3 (3-4)	5 (4-6)	7 (7-8)	H=52.9, p<0.001
Nestling mortality 1-3 days	0 (0-0)	0 (0-0)	0 (0-0)	H=1.91, p=0.38
Nestling mortality 3-7 days	0 (0-0)	0 (0-1)	0 (0-1)	H=4.44, p=0.11
Nestling mortality 7-9 days	0 (0-0)	0 (0-0)	0 (0-1)	H=5.04, p=0.08
Nestling mortality 9-11 days	0 (0-0)	0 (0-1)	0 (0-1)	H=4.47, P=0.11
Nestling mortality 11-13 days	0 (0-0)	0 (0-0)	0 (0-0)	H=2.11, p=0.35
% Nestling mortality 1-7 days	0 (0-0)	0 (0-20)	0 (0-20)	H=1.69, p=0.43
% Nestling mortality 7-13 days	0 (0-0)	8.3 (0-40)	28.6 (0-100)	H=7.72, p=0.021
% Total nestling mortality	0 (0-33)	29.2 (0-100)	100 (28.6-100)	H=20, p<0.001
Fledged young	3 (2-3)	3.5 (0-5)	0 (0-5)	H=1.68, p=0.43
Fledgling tarsus length (mm)	17.01 $\pm$ 0.14	16.78 $\pm$ 0.13	16.56 $\pm$ 0.18	F=2.06, p=0.14
Fledgling mass (g)	13.77 $\pm$ 0.28	12.60 $\pm$ 0.27	12.22 $\pm$ 0.37	F=6.93, p=0.002
Fledgling wing length (mm)	42.5 $\pm$ 0.8	41.4 $\pm$ 0.8	38.4 $\pm$ 1.1	F=4.61, p=0.015

425

426 **Figure legends**

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428 **Figure 1.** Minimum temperatures near the study area for the period 20 April-10 May for
429 2010 (open dots) and for 1991-2014 excluding 2010 (means as filled symbols $\pm$ 95%
430 confidence intervals)

431 **Figure 2.** Correlations between hatching date (April 1=1) and a) number of fledglings
432 (Kendall $\tau_{71}=0.17$, $p<0.05$) and b) nestling mortality in the second week of life (Kendall
433 $\tau_{71}=-0.30$, $p<0.05$)

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439 Figure 1

Figure 2