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Climate effects on breeding phenology of Peregrine and Lanner Falcons in the Mediterranean

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We explored the effects of weather on the timing and reproduction of the Mediterranean Peregrine Falcon *Falco peregrinus brookei* and the Lanner Falcon *F. biarmicus feldeggii* living on the Mediterranean island of Sicily. We found that the start date of incubation has changed during 1979–2019 and analysed whether incubation timing affected the productivity of both populations and whether the change of incubation date and the quality of breeding sites depended on climatic conditions. Overall spring temperature and rainfall increased on Sicily and the incubation date of the Peregrine and the Lanner Falcon has shifted to be about one week later over the time period 1979 to 2019. Linear mixed modelling showed the influence of winter conditions and random effects (climate sector of island, year of study) on incubation date in both species. The increase in February rainfall has delayed incubation in the Peregrine Falcon, while we could not identify a specific monthly effect delaying incubation in the Lanner Falcon. In both species, the shift in incubation date has resulted in a decrease in productivity (number of fledglings). Weather conditions in late spring predicted the quality of the breeding site of Lanner Falcons but not of Peregrines. The breeding phenology of both falcons shows a common response to weather conditions on Sicily, however the Lanner Falcon seems more sensitive than the Peregrine to the changing climate. Climate effects add to other anthropogenic impacts negatively affecting the future survival of this insular population, which is the largest in Europe.

Key words: Lanner Falcon, Mediterranean Peregrine Falcon, population productivity, incubation onset, weather effect

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Changes in regional climates can impact avian populations and increase the risk of local extinction (Sekercioglu *et al.* 2008, Cahill *et al.* 2013, de Moraes *et al.* 2020). In birds, climate change is mainly triggering distributional shifts (e.g. Thomas 2010, Burrows *et al.* 2014), migratory phenology and trait changes (e.g. Both & te Marvelde 2007, Lehikoinen & Sparks 2010, Saino *et al.* 2011) and affecting viability of populations (e.g. Both *et al.* 2006, Dunn & Winkler 2010). Furthermore, climate change has prompted research into the complex and interrelated effects it can have on reproductive performance (reviewed in Dunn & Winkler 2010). Effects of climate change have been observed on the onset of incubation and on hatching success (Stoleson & Beissinger 1995), incubation behaviour (Coe *et al.* 2015, DuRant *et al.* 2019), variation in clutch size (Both & Visser 2005) and productivity (Meller *et al.* 2018). Furthermore, they can create a mismatch with food availability (Hällfors *et al.* 2020). Despite the extensive documentation on how climate impacts the behaviour and ecology of birds (see for instance Sharp *et al.* 2020), the effects of climate changes on large raptors have been less documented (Dunn & Winkler 2010), while there is a bias towards migratory species living in boreal ecosystems at northern latitudes (e.g. Halupka & Halupka 2017, Meller *et al.* 2018, Hällfors *et al.* 2020).

The Mediterranean Basin is one of the areas of the

Figure 1. (A) Mediterranean Peregrine *Falco peregrinus brookei* landing on its roost (photo Domenico Margarese, 7 April 2019, Province of Palermo). (B) European Lanner Falcon *Falco biarmicus feldeggii* entering its nest (photo Angelo Nardo, 11 May 2020, Province of Agrigento).

world suffering the largest impacts of climate change (IPCC 2015), and in Mediterranean areas of Italy the climate is becoming warmer and drier with more concentrated and intense rainfall (Giorgi & Lionello 2008, Provenzale 2009). In these areas, unpredictable time-series of increased spring precipitations are occurring more often (De Vita & Fabbroncino 2007, Drago 2010). Climate warming also involves variation in parameters other than temperature, in particular rainfall (IPCC 2015). This multifaceted process is expected to expand breeding ranges northward, as well as alter demographic trends, for bird species that live in Mediterranean xeric ecosystems (Huntley *et al.* 2007, Morganti *et al.* 2017, Herrando *et al.* 2018).

Raptors are a large and variably assorted group of charismatic top-level predators, which are of high conservation concern and play a key-role in ecosystem functioning (Sergio *et al.* 2006, 2008, Donázar *et al.* 2016). Raptors are particularly responsive to climate variation: on a continental scale, populations of several species are totally or partially migratory or sedentary depending on the latitude where they live (Newton 1979, Ferguson-Lee & Christie 2001) and species adjust the phenology of migration in response to alterations of the temperature regime (Jaffré *et al.* 2013). At a local scale, the weather during winter, before egg formation, largely affects the number of breeding pairs in a population (Koztrzewa & Kostrzewa 1990). In addition, laying and incubation dates, chick survival and reproductive success depend on the levels of rainfall (Ratcliffe 1984, Mearns & Newton 1988, Rodríguez & Bustamante 2003, Anctil *et al.* 2014, Zuberogoitia *et al.* 2018, Morganti *et al.* 2019), low temperatures and on extreme weather events (Watson 2009, Morganti *et al.* 2017, Carlzon *et al.* 2018) experienced during the breeding season or during consecutive years. Furthermore, climate is affecting food and often is a factor determining a lack of variety and low density and accessibility of prey (Mearns & Newton 1988, Steenhof *et al.* 1997, Wiens *et al.* 2006).

We investigated effects of long-term weather changes on the timing and reproduction of two large falcon species, the Mediterranean Peregrine Falcon *Falco peregrinus brookei*, hereafter Peregrine) and the European subspecies of the Lanner Falcon *F. biarmicus feldeggii* (Figure 1), sympatrically living on Sicily, the largest Mediterranean island. Information about the effects of climate on the timing of reproduction and reproductive performance is available mostly for European and Siberian Peregrine populations (Ratcliffe 1984, Mearns & Newton 1988, Anctil *et al.* 2014, Carlzon *et al.* 2018) or Mediterranean populations living in northern Spain (Zuberogoitia *et al.* 2018), while to the best of our knowledge there is no research focusing on the effects of climate on the reproduction of Lanner Falcons in Europe.

We first documented the long-term (1979–2019) temperature and rainfall changes during the breeding season of both falcons on Sicily and analysed whether the timing of reproduction, described as the date of incubation onset, has changed during that period. Subsequently we analysed whether incubation timing affected the productivity of both populations and whether change in incubation onset depended on climatic conditions. Finally, we examined the effect of climatic conditions on the quality of breeding sites in terms of productivity.

METHODS

Study area

Sicily was selected as the study area representative of the Mediterranean bioclimate in Southern Europe occupied by Peregrine and Lanner Falcons (Figure 2). The island covers 25,832 km^2 and is the largest (8.6% of national surface) and one of the most populated (192.3 inhabitants per km^2) administrative regions of Italy, from which it is separated by the 3-km-wide Strait of Messina. Almost 24.4% of the territory is mountainous, 61.4% is composed of highlands and 14.2% of the surface is lowland. Natural deciduous forests and Mediterranean vegetation have been greatly reduced by centuries of anthropogenic impact and forests occupy only 8% of the territory, mostly in the north-eastern part of the island, with European Beech *Fagus sylvatica* forests extending from 1200–1400 m a.s.l. at the northern ridge and endemic Birch *Betula aetnensis* on the slopes of the Aetna volcano between 1300 and 2100 m a.s.l. There is considerable habitat heterogeneity in hilly and flat inland areas, where cultivation zones (especially arable land with cereals and fodder, currently replaced by vineyards and olive orchards) alternate with woodlots of non-native species (*Pinus* spp. and *Eucalyptus* spp.), natural oak *Quercus* spp. evergreen woods, Mediterranean xeric grasslands and shrub vegetation. The climate is typically Mediterranean, but shows considerable variation between the higher and wettest northern areas (>1000 mm/year), which mostly fall within the sub-humid and dry meso-Mediterranean bioclimates, to the less elevated and arid (<500 mm/year) south-eastern areas which mostly fall into the thermo-Mediterranean dry bioclimate.

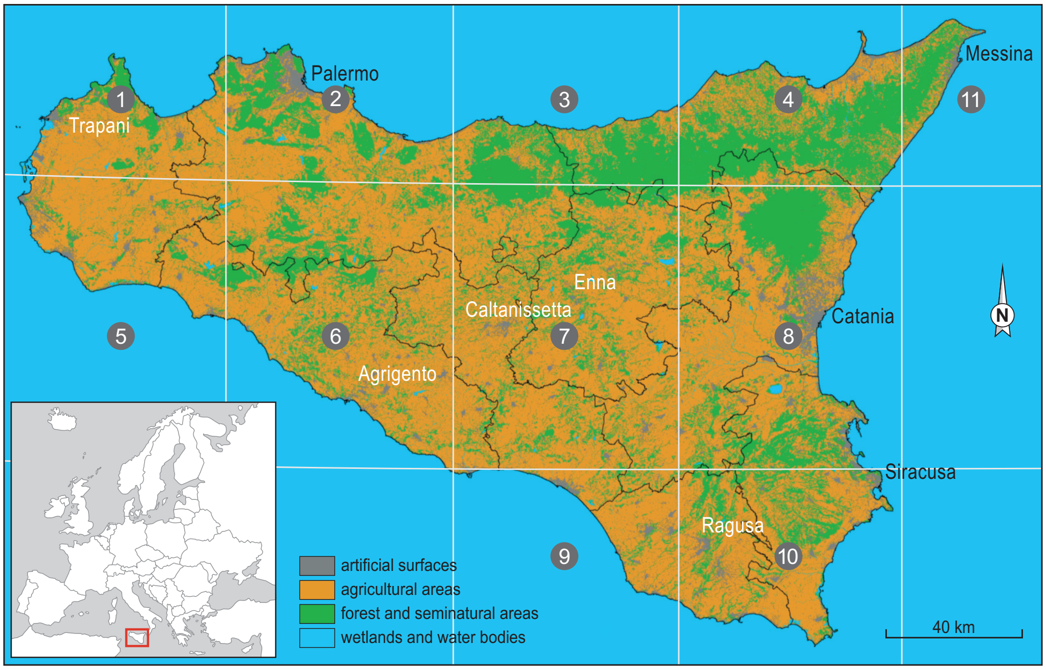

Figure 2. Map of Sicily showing the main habitats and major cities and subdivision into the 11 ERA-Interim cells used to extract weather data corresponding to the breeding sites of Peregrine and Lanner Falcons. ERA-Interim cells have size of 0.75° latitude × 0.75° longitude.

Study species

The Sicilian population of the nearly-cosmopolitan Peregrine is currently assigned to the Mediterranean subspecies *brookei* (White *et al.* 2013). Peregrines are quite common in Sicily, and in recent years (2010–2019) the population is quite stable with some 260 pairs spread across the main island, plus some 13–15 pairs living in the small neighboring islands (Sarà 2008, Sarà *et al.* 2021). The population is not distributed at random but concentrated in all the suitable inland and coastal habitats of the island, nesting in either small crags and large cliffs from sea level to 1424 m a.s.l., but it is rarer in the densely forested habitats of the north-eastern ridge (Peloritani, Nebrodi, Aetna). Biologging (Bondì *et al.* 2018) and genetic data (Mengoni *et al.* 2018) reveal a fairly closed population with limited dispersion outside the island. Illegal shooting, poisoning, electrocution and collision with electricity wires and wind turbines are the main causes of unnatural mortality. Annually a small number of nests is raided for illegal trading of eggs and chicks (Sarà *et al.* 2021).

The largest European population of the Lanner Falcon is found on Sicily, but its range extends to continental Italy, Greece and the Balkans (Ferguson-Lees & Christie 2001, Leonardi 2015). The Lanner Falcon is also a top predator, which breeds in small to medium crags and cliffs disseminated between open Mediterranean steppe-like habitats of central and southern Sicily, from 100 to 900 m a.s.l. It is absent or very rare in north-eastern Sicily. The Italian population has an unfavourable conservation status for its restricted range and also because it is rapidly declining. The Italian population has more than halved in the last 20 years and today is estimated at around 60–80 pairs (Andreotti & Leonardi 2007, Brichetti & Fracasso 2020). Degradation and fragmentation of Mediterranean steppe-like habitats (Sarà 2014) and the large unnatural mortality of adults and young due to illegal shooting, poisoning, electrocution and collision with wind turbines and electricity wires, plus the illegal trading of eggs and chicks, are the main causes of population decline (Di Vittorio *et al.* 2017).

Monitoring falcon territories

A consistent part of the Peregrine and Lanner Falcon populations of Sicily were continuously monitored from 2010 to 2019. Two of us (MS and LZ) focused more on following the northern and western populations, while AN and RM mostly followed the southern and eastern populations of both species. Authors, all experienced observers, carried out all the fieldwork, scanning cliffs and their occupants with 10×42 binoculars and 20–60× telescopes and from vantage points located far enough to minimize disturbance to the nesting birds. Furthermore, the two falcons were studied in the past; Peregrine data were collected by Schenk *et al.* (1983) and Mascara (2012), while data on Lanner Falcons was obtained from Ciaccio *et al.* (1987), Massa *et al.* (1991), Mascara (2012) and Mascara & Nardo (2018), enabling us to obtain historic data on breeding birds in 1979–2009. Once non-reproductive (territorial) pairs were excluded, raw data from the past (1979–2009) and current (2010–2019) monitoring were pooled to form a database of reproductive events for each species. Falcon monitoring in Sicily always followed standard protocols (e.g. Steenhof & Newton 2007) which guaranteed a fairly homogeneous collection of breeding data over time. This protocol considered a breeding territory to be occupied if a pair of adult Peregrines or Lanner Falcons were resident during the breeding season and nests were considered active if eggs or young were detected during the season. Successful nests were those with ≥ 1 nestling surviving to fledging or those in which large and well feathered young were observed (80% rule in Steenhof & Newton 2007). The protocol provided for three to six visits at each territory, which covered all the breeding activities of falcon pairs in the season. Visits usually started from the moment of territorial reinforcement, courtship and mating (mid-January to early February) and were repeated during egg-laying and incubation (mid-February – early April) and then hatching, brooding and fledging (mid-April – mid-June), using preferably the early morning and late afternoon hours of clear and non-rainy days, but changing the monitoring timetable of each territory from one visit to another. From 2014 to 2018, a sample of nests (13 Lanner Falcon, 27 Peregrine) was monitored with more repeated visits, thus accurately determining the start of incubation, hatching date and the development stages of the chicks, in order to determine the correct date of ringing and tagging with satellite transmitters (Bondì *et al.* 2018, Sarà *et al.* 2019). This sample was used to estimate the start of incubation, by means of backdating, of all the other sites controlled with the standard protocol (see above) or past data where only fledging dates were usually known. For backdating the Peregrine incubation onset, we assumed an average of 32 days for incubation and of 40 days for fledging (Newton 1979, own unpubl. data), while for the Lanner Falcon we assumed an average of 33 days for incubation and of 45 days for fledging (Leonardi 2015, own unpubl. data).

The incubation onset was measured in Julian days starting from 1 equalling 1 January, and is referred to as incubation date (ID). The breeding outcome of the two falcon populations was expressed as: (1) productivity, i.e. number of fledglings per pair, including both successful and unsuccessful pairs (Steenhof & Newton 2007), and (2) breeding quality index (BQI), as estimator of the annual performance of each territory. BQI was obtained by centring the annual productivity value of each site by the annual average of studied sites (Ferrer & Bisson 2003, Zabala & Zuberogoitia 2014). High-quality sites have BQIs > annual average, medium sites have BQIs = annual average and low-quality sites have values < annual average.

Data processing and analysis

Climate data, namely the monthly means of soil temperature (°C) and cumulated precipitation (mm) were measured at the surface level and extracted from the Era-Interim archives of the European Centre for Medium Range Forecasts (Simmons *et al.* 2006). The use of ERA-Interim data reflects the average climatic variation over the whole island and this data was preferred over local weather stations because the latter are much less complete in time and spatial coverage. Climate data were in GRIB format and were extrapolated and projected on Sicily using a Q-GIS plug-in. Five months (January–May), pertinent to the breeding biology of the two focal species, were extracted per year of the historical time-series 1979–2019 with a spatial resolution of 0.75° latitude × 0.75° longitude. This spatial resolution divided Sicily into 11 ERA-Interim cells of 83.25 km in latitude × 66.75 km in longitude, however this included sea in the coastal cells (Figure 2). Georeferenced breeding sites were allocated to the pertinent ERA-Interim cell to assign the monthly (January–May) temperatures and precipitations to the studied sites. The ERA-Interim cells therefore correspond to 'climate sectors', in which breeding sites that share similar climatic conditions over time are grouped. This enabled comparison of modelling performance between climatically homogeneous sites. Six cells enclosed all the studied sites of the Lanner Falcons and nine those of the Peregrines. On average, the central and north-eastern areas are the coldest and rainiest of Sicily (climate sectors 3, 4, 7 and 8). Sector 11, the extreme north-eastern Peloritani corner was not included due to the lack of studied sites. Climate sectors 1, 5 and 9 are the mildest and driest and the sectors 2 and 6 (plus 10, the Iblean plateau, not considered for the lack of studied sites) show an intermediate situation (Figure 2). Climate data per cell and per month were centred by subtracting the long-term

(40-years) mean for the same month and cell. This allowed expressing temperatures and rainfalls as deviations from the average conditions of the climate sectors (Table S1, Figure S1).

We performed a systematic data exploration before testing models, to reduce the probability of false outcomes (i.e. increase of type I or type II errors; Zuur *et al.* 2010). Outliers present in the monthly climate data were not omitted, because they could represent exceptional events of varying temperatures or rainfall worthy of inspection and modelling (Schielzeth 2010). Analysis of the box plots revealed no outliers in the Lanner Falcon IDs and only three in the Peregrine IDs, corresponding to unusually early incubation dates (3, 10 and 12 February) in 1979–80, which were removed from the analysis. After the data exploration, the Peregrine had a more complete dataset with 255 reproduction events complete with incubation start date, while the dataset of Lanner Falcon reproduction events with incubation dates was nearly half that of the Peregrine (n = 125). Explanatory variables were centred and standardized to improve the interpretability of regression coefficients and to produce standardized slopes comparable in magnitude within and between models (Schielzeth 2010). The check for collinearity did not detect any VIF ≥ 3 in the explanatory variables. We have also dealt with over-parametrization problems, limiting the number of predictors with their interactions to the most meaningful ones, hence with ratios $n/k \geq 10$, where k is the number of model parameters to be estimated (e.g. one for each predictor and their interactions plus one for the intercept) and n the number of observations (Harrison *et al.* 2018).

The first step of our study was the examination of the patterns of temperature and rainfall in the climate sectors of Sicily in which reproduction data were available. First-order serial correlations (autocorrelation with data lagging one year, AR1) of residuals in the climate variables were inspected by the Box-Ljiung Q statistic. The patterns of temperatures and rainfalls in the five months important for species' reproduction and per every climate sector were then produced by Prais-Winsten regression, appropriate for time-series (Hammer *et al.* 2001, Hammer 2021; Table S1, Figure S1).

The second step was the verification of the observed variation in the timing of ID of both species. For the period 1986–1999 there is a lack of reproduction data that include the start dates of incubation of both species. Therefore, to describe the ID trend over time, it was necessary to verify whether a linear fit was more adequate than a non-linear fit. The Akaike Information Criterion corrected for small sample (AIC_c) was used in the selection of the model. Lower AIC values imply a better fit, adjusted for the number of parameters (Akaike 1974).

The unbalanced sample of ID data forced us to group the incubation dates of both species in 5-year periods; we used a Kruskal-Wallis ANOVA and post-hoc test on the median start date of incubation.

Once it was verified that the weather in the study areas and the incubation onset of both species changed over time, we employed linear mixed models with a normal distribution of errors (LMM; Harrison *et al.* 2018), to first test the effect of the timing of incubation on productivity. Productivity was the response variable, ID a predictor with a fixed effect and year and climate sector (id of ERA-Interim cells) added as categorical variables with a random effect, to account for variability in productivity between years and climate sectors. We tested the response of incubation time to changing weather conditions also using a LMM with a normal error distribution. Lastly, we tested whether weather conditions influenced the breeding productivity (BQI). Since BQI is calculated from the productivity values, there is a strong collinearity between them (VIF = 4.45 for Lanner Falcon and VIF = 8.19 for Peregrine). However, these two response variables were employed in separate LMMs. Productivity was used to measure the biological response of each species to variation in incubation date, while BQI was used to test the effect of changes in weather conditions on the productivity of breeding site. In LMMs, coding of categorical predictors was performed using an over-parameterized model and hypotheses were tested with type III decomposition useful for factorial designs with unequal n values.

Monthly precipitation and soil temperature values were standardized (mean = 0 and SD = 1) and added as fixed effects in analyses, while year and climate sector functioned as categorical random effect variables. Models testing effects on BQI did not include the random effect of year because the index already controls for annual random variability (Ferrer & Bisson 2003). Instead the ID of the site was entered as a nested random factor in the climate sector to take the effect of territory into account. Models' adequacy, i.e. check of normality and homoscedasticity, was evaluated by examining the normal P-P plot and the scatterplot of standardized residuals versus standardized predicted values, respectively.

For every LMM, the Whole Model F-test of significance on the R^2_{adj} value was used to measure the models' goodness-of-fit and the joint effect of all predictors on the response variable. The beta coefficients (standardized slopes) estimated the direction and extent of change (in standard deviation units) of the predictor of interest on the response (while all other predictors in the model are being controlled for, i.e. statistically held constant). Although random effects in LMMs complicate the use of standardized slopes as standardized size effects (see Schielzeth 2010), the response will increase or decrease by the (positive or negative) value of the beta coefficient for every 1 SD unit increase in the fixed predictive variable.

The effect of climate conditions on ID of the two species was tested only for the months of January–March (pre-laying, laying and incubation stage, hereafter called early season model), as climate conditions during April and May of the same year (hatching, brooding and fledging stage, hereafter called late season model) cannot influence the start of incubation. The effect of climate conditions on BQI was tested in the early season and late season models. Effects of the interaction between temperature and rainfall in each month were also entered in both models. The threshold for statistical significance was set at $P < 0.05$, and means ± SE were reported. Statistics were computed in STATISTICA v. 10.0 (www.statsoft.com) and PAST v. 4.09 (Hammer 2021).

RESULTS

Weather changes

Monthly average temperatures and precipitation rates showed a tendency to deviate from averages calculated in the 40-year period (Figure S1). The rainfall patterns of February and March increased simultaneously in all climatic sectors occupied by the falcons, as shown by the close overlap of the linear fitting coefficients estimated by a Prais-Winsten regression (Figure S1A); while precipitation in January and May was more variable between climate sectors, with western areas receiving much more rain than the 40-years average, and eastern areas receiving less or equal volumes of rain to the 40-years average. April was bucking the trend as some western areas received less rain than the 40-years average, while the other areas received a similar volume of rain (Figure S1A). Temperature variation was much more regular and increased in all the five months (Figure S1B). The scatter of the Prais-Winsten linear fit was however more homogeneous in January and relatively less so in the other months. Also here, April showed the most striking variation, with a steeper linear fit in some central-eastern sectors. Three sectors showed statistically significant serial correlation, but were considered to contribute a negligible bias to modelling this monthly effect.

Reproductive phenology changes

In both species we see a tendency to delay the incubation date over the course of the study-period (Table 1, Figure 3). The Peregrine's incubation date correlates with year (r = 0.290, n = 255, P = 0.000), increasing over time according to a linear relationship of $y = 0.1821 \times x - 299.61$ (Figure 3A). The linear fit to the data is better ($\mathrm{AIC_c}$ = 13,924) than the non-linear quadratic fit ($\mathrm{AIC_c}$ = 14,446). Similarly, the incubation date of Lanner Falcons was correlated with year in the study period (Pearson r = 0.314, n = 125, P = 0.0004) with a linear relationship of $y = 0.2584 \times x - 456.76$ (Figure 3B), which also has a better fit ($\mathrm{AIC_c}$ = 10,483) than the quadratic regression ($\mathrm{AIC_c}$ = 11,151). The median date of incubation onset in Peregrines was 2 March in 1976–80 and 8 March in 2015–19, with an incubation delay of 5–8 days (Q25–Q75 quartiles;

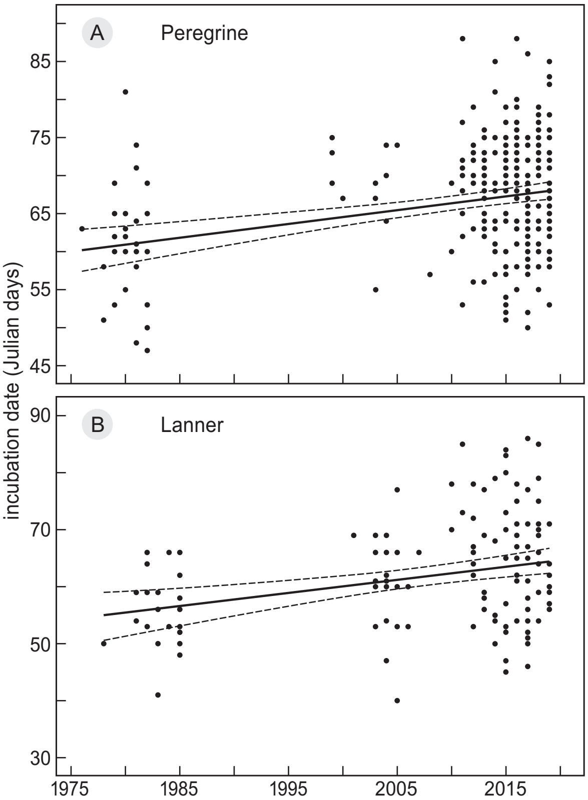

Figure 3. Delay of start of incubation over the years of Lanner and Peregrine Falcons breeding on Sicily. Scatterplot of incubation dates in Julian days against year in (A) Peregrine and (B) Lanner Falcon. Linear fit (solid line) and 95% confidence limits (dashed lines).

Table 1). This change was statistically significant between pentads (Kruskal-Wallis Anova $H_{5,255} = 25.811$, $P < 0.001$). Post-hoc analysis indicated that the change mainly occurred between the 1976–80 and the 2010–14 pentad ($z = 3.346$, $P = 0.012$) and between the 1976–80 and the 2015–19 pentad ($z = 2.983$, $P = 0.043$). Less strong changes occurred between 1981–85 and 2000–04 ($z = 2.936$, $P = 0.05$), between 1981–85 and 2010–14 ($z = 3.989$, $P = 0.001$) and between 1981–85 and 2015–19 ($z = 3.670$, $P = 0.004$).

Similarly, in the Lanner Falcons, the median date of incubation onset was delayed by a week from 25 February in 1981–85 to 3 March in 2015–2019, with the Q25–Q75 quartiles indicating a range of 6–13 days of delay (Table 1). The changes differed between pentads (Kruskal-Wallis Anova $H_{4,132} = 14.890$, $P = 0.005$) and occurred chiefly between the 1981–85 and the 2010–14 pentad ($z = 3.405$, $P = 0.007$) and between the 1981–85 and the 2015–19 pentad ($z = 3.226$, $P = 0.013$).

The effect of incubation date on productivity

Productivity of the Peregrine population was affected by all tested predictors ($R^2_{adj} = 0.078$, $F_{28,222} = 1.758$, $P = 0.014$). Productivity is predicted by the incubation date with a negative relationship (beta coefficient$_{ID}$ = –0.229 ± 0.071, CL95 range: –0.369 – –0.088; Figure 4A), that corresponds to a decline of 0.229 SD units of productivity for each 1 SD unit increase in the incuba-

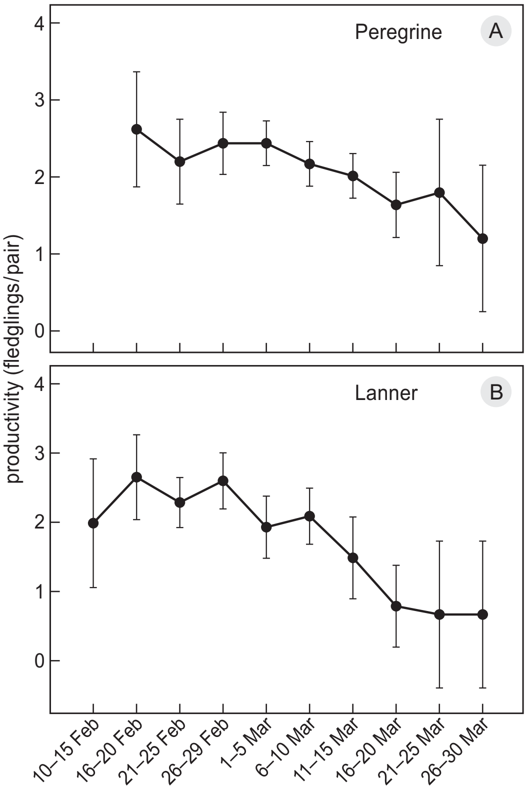

Figure 4. Expected population marginal means, given the best model (Table 2), showing the decline in productivity as an effect of the increasing delay in the initiation of incubation (in 5-day periods) of (A) Peregrine and (B) Lanner Falcons. Vertical bars denote 95% confidence intervals.

Table 1. Median dates of incubation onset in Lanner Falcons and Peregrines on Sicily. Q25 is the first quartile and Q75 the third quartile date of incubation onset. Time lapse is the number of days between the earliest to the latest date.

	1976–80	1981–85	2000–04	2005–09	2010–14	2015–19	Total
Peregrine							
Median date	02 Mar	01 Mar	10 Mar	07 Mar	10 Mar	08 Mar	08 Mar
Q25	27 Feb	22 Feb	08 Mar	26 Feb	04 Mar	03 Mar	02 Mar
Q75	05 Mar	05 Mar	14 Mar	15 Mar	13 Mar	13 Mar	13 Mar
Earliest date	20 Feb	16 Feb	24 Feb	26 Feb	22 Feb	19 Feb	16 Feb
Latest date	22 Mar	15 Mar	16 Mar	15 Mar	29 Mar	29 Mar	29 Mar
Time lapse (d)	30	27	20	17	35	38	41
n	16	17	10	2	59	151	255
Lanner Falcon							
Median date	–	25 Feb	02 Mar	01 Mar	08 Mar	03 Mar	01 Mar
Q25	–	19 Feb	01 Mar	23 Feb	25 Feb	25 Feb	23 Feb
Q75	–	28 Feb	07 Mar	07 Mar	14 Mar	12 Mar	09 Mar
Earliest date	–	10 Feb	16 Feb	09 Feb	19 Feb	14 Feb	09 Feb
Latest date	–	07 Mar	10 Mar	18 Mar	26 Mar	26 Mar	26 Mar
Time lapse (d)	–	25	22	37	35	41	46
n	–	23	19	13	22	55	132

tion onset date (Table 2). The random effects of climate sector ($F_8 = 1.666$, $P = 0.108$) and year ($F_{19} = 1.012$, $P = 0.448$) are not significant. Overall, two-third of the Peregrine incubation dates lay within the first half of March, and nearly 19.6% in the second half of February and 13.7% in the second half of March.

Also in the case of the Lanner Falcon, all predictors had a significant joint effect on productivity ($R^2_{adj} = 0.380$, $F_{27,97} = 3.815$, $P = 0.000$). Productivity is negatively related with incubation date (beta coefficient$_{ID}$ = –0.323 ± 0.095, CL95 range: –0.511 – –0.135; Figure 4B), with a decline of 0.323 SD units in productivity for each 1SD unit increase in the incubation onset date. The random effect of climate sector is also significant, due to higher productivity in climate sectors 6–8 compared to climate sector 2 (Tukey Unequal N HSD post-hoc test), while year has no significant effect ($F_{21} = 1.567$, $P = 0.074$). In the sample, more than 45% of Lanner Falcon incubation dates fell in the second half of February and 38.4% in the first half of March. The tails of incubation dates extended to the first half of February (3.2%) and the second half of March (12.8%).

Table 2. Statistics of a linear mixed model showing significant effects on productivity of Lanner Falcons and Peregrines on Sicily. Non-significant effects have been omitted. *df* = degree of freedom.

	Effect	*df*	*F*	*P*
Peregrine				
Intercept	Fixed	1	183.838	<0.001
Incubation date	Fixed	1	10.255	0.002
Lanner Falcon				
Intercept	Fixed	1	51.891	<0.001
Climate sector	Random	5	4.883	0.001
Incubation date	Fixed	1	11.602	0.001

Table 3. Statistics of a linear mixed model estimating climate effects in the early breeding season (January–March) on incubation onset of Peregrines on Sicily. Model specifications and abbreviations as in Table 3.

	Effect	*df*	*F*	*P*
Intercept	Fixed	1	3.234	0.076
February rainfall	Fixed	1	4.054	0.045
Climate sector	Random	8	2.372	0.018
Year	Random	19	2.391	0.001

The effect of weather conditions on incubation onset

The Whole Model *F*-test of the LMM showed a joint statistical effect of winter climate conditions and random effects on incubation onset of Peregrines ($R^2_{adj} = 0.225$, $F_{36,214} = 3.018$, $P < 0.001$). The random effects of year and climate sector were statistically significant (Table 3). Rainfall in February was the only significant fixed effect, its beta coefficient (–0.661 ± 0.328, CL95 range: –1.309 – –0.014) showed a negative relationship with incubation onset, with a decrease (advance) of 0.661 SD units in incubation dates for each 1 SD unit decrease in February precipitation. In the case of Lanner Falcons, the Whole Model *F*-test was significant ($R^2_{adj} = 0.310$, $F_{35,89} = 2.589$, $P = 0.000$), but none of the fixed and random predictors entered in the model were individually significant. This result shows that winter conditions and random factors only have a joint effect on the incubation dates of this species.

The effect of weather conditions on the quality of breeding site

The Whole Model F-test did not show any significant effect of the predictor variables on the Peregrine's BQI ($R^2_{adj} = 0.100$, $F_{112,138} = 1.248$, $P = 0.108$), so none of the random factors and climatic variables of the early season model have a significant effect on the quality of breeding sites. Also the late season model detected no significant effect of the predictor variables on the Peregrine's BQI ($R^2_{adj} = 0.116$, $F_{109,141} = 1.302$, $P = 0.070$), and random factors and climatic variables in the late season model of BQI were not significant either.

In the case of Lanner Falcon, the model results are practically the same for the early season model, which showed no significant effects of the variables on BQI ($R^2_{adj} = 0.151$, $F_{57,67} = 1.386$, $P = 0.100$), and no significant effects of the random and fixed predictors. In contrast, the late season model indicated a significant effect of all variables on the Lanner Falcons' BQI ($R^2_{adj} = 0.325$, $F_{54,69} = 2.095$, $P = 0.002$), along with significant effects of climate sector ($F = 2.503$, $P = 0.036$) and May precipitation ($F = 5.087$, $P = 0.027$; Figure 5).

DISCUSSION

Climate conditions in Italy, as documented in the last 15–20 years, are changing (Provenzale 2009). Temperature shows an average increase of 0.09°C per 10 years

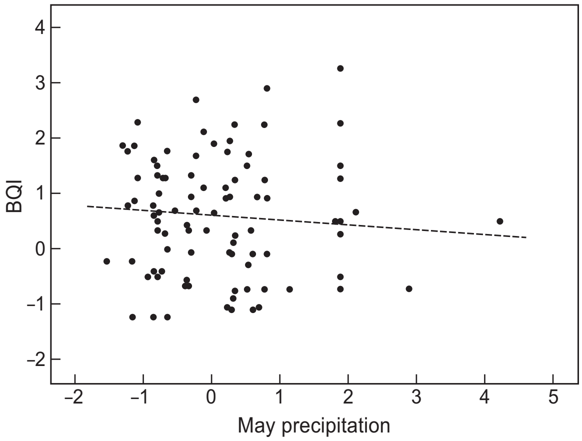

Figure 5. The inverse relationship between the Lanner Falcon breeding quality index (BQI) and May precipitation (mm/year). BQI and May precipitation values have been standardized (mean = 0 and SD = 1).

and an average rainfall decrease of 4.7% per 10 years (Zenatello *et al.* 2014) and climate change in Sicily is consistent with this overall trend (Viola *et al.* 2014, Zenatello *et al.* 2014, ISPRA 2019). Likewise, the precipitation regime in Sicily has changed, and rains occur much more frequently in spring, when they can be brief and particularly violent (De Vita & Fabbroncino 2007, Drago 2010, ISPRA 2019). Climate ERA-Interim data used in this study show linear trends of change in the last 40 years; overall the falcons are experiencing increasingly wetter and warmer conditions during February–March (egg-laying and incubation) and May (late brood raising and fledging) and a drier and warmer climate in January (courtship displays and territorial reinforcement) and April (hatching and early brood raising), although the change seems more pronounced in some climate sectors of the island than in others. Linear climate change fits well with the available data on the reproductive phenology of both species, supporting the progressive delay of incubation onset found in this study. However, the possibility of fluctuations in the incubation dates of both species cannot be excluded, because data for the 1986–1999 breeding period are lacking, suggesting some caution in our findings. While keeping this limitation in mind, we have found that the incubation onset of the Peregrine and of the Lanner Falcon was delayed about one week from 1979 to 2019. We showed an overall influence of winter conditions and the random effects of the year and the climate sector on incubation onset of the two species. Both models fitted better (i.e. statistically significant Whole Model *F*-Tests) than constant response probabilities (intercept-only models). Model statistics show a more than acceptable model fit and underline a stronger joint effect of predictors on the incubation onset of the Lanner Falcon ($R^2_{\text{adj}} = 0.310$) than that of the Peregrine ($R^2_{\text{adj}} = 0.225$). The increase in rainfall in February would explicitly affect the start of the Peregrine's incubation, while no specific monthly effects would affect the delay in the start of incubation in the Lanner Falcons.

In most avian species breeding performance decreases over the season, with early birds having more success and higher productivity than late conspecifics (Verhulst & Nilsson 2008) and individuals born early in the season are generally more likely to survive and recruit (Wiens *et al.* 2006, Nisbet *et al.* 2016). Consistent with this, both species show a negative response in productivity to the delay of incubation onset. In the Peregrine this happens without an effect of year and of climate sector, which in turn suggests that the effect of incubation date on the productivity of this species is homogeneously distributed over time and on the population living on the whole island. Lanner Falcons share with Peregrines the lack of significance of year, while incubation date contributes together with climate sector to lower productivity in some areas (the northern sector 2, which is at the edge of the species' range) compared to others (the central-southern sectors 6–8 in the species' core range).

Incubation date could also depend on the quality of the habitat or of the mates at a given site (McCleery *et al.* 2008). Such differences will certainly be present in the populations of both species, because older and more experienced birds are generally more inclined to lay earlier than younger and less experienced birds (at least for the Peregrine, see Zabala & Zuberogoitia 2014, 2015). Aside from these factors not yet studied in our area, our results suggest a tendency in populations to reproduce later in recent years due to climatic effects.

The combined results of modelling the effect of weather conditions on incubation onset and productivity tell us that there is no direct effect of climate on Peregrine productivity in its Mediterranean habitat. Rather, the effect of weather would be mediated and climate change would then trigger a chain of events by delaying the onset of incubation, which in turn affects the productivity of this species. Instead the Lanner Falcon would only suffer the consequences of a general change of climate on incubation onset, without any specific monthly effect of temperature or precipitation.

To best contextualize our results, we must start from the fact that females of large raptors need to reach an optimal body condition in order to start reproduction and produce eggs (Newton 1979). The body's energy reserves are usually acquired in the weeks or months before laying begins and then continue with incubation. Food supply is the ultimate factor for breeding at a given time, while day length is the proximate factor that brings the individual into condition at the appropriate date (Newton 1979, Dunn & Winkler 2010). This means that temperature and rainfall are not among the primary cues used in these species to initiate reproduction, but they can be a direct or indirect constraint for timing activities. Cold weather can directly affect the timing of reproduction by requiring a higher energy demand for females and, in turn, eliciting a greater investment solely for body maintenance at the expense of egg production and/or the accumulation of fat reserves before the long incubation period. This occurs for instance in Golden Eagles *Aquila chrysaetos* of western Scotland, where laying was significantly later in years when February was colder than average (Watson 2009). This situation is unlikely at Sicilian latitudes and could only occur just in some inland mountain areas occupied by a few pairs of Peregrines. The indirect constraints that often act through the effects of rainfall on food supply seem more plausible. Weather interacted with prey affecting the Golden Eagle's reproductive rates (Steenhof *et al.* 1997); and in a suite of European species, including the Peregrine, negative relationships between breeding success and rainfall have been observed (see references in Newton 1998 and in Watson 2009). Generally, rainfall affects the reproductive performance of raptors by reducing their food supply and by suppressing hunting behaviour and foraging success. Prey can be either less accessible and less abundant during rainy days (Aoyama *et al.* 1988), although Olsen & Olsen (1992) reported that rain does not hamper hunting in Peregrines. Heavy rain downpours are the main cause of reproductive failure and mortality amongst adult female Brown Falcons *Falco berigora* in Australia (MacDonald *et al.* 2004). In northern latitudes, the effects were mediated not so much by reduced hunting success, but by soaking or chilling of eggs and chicks in exposed Peregrine nests (e.g. Carlzon *et al.* 2008, Anctil *et al.* 2014, Zuberogoitia *et al.* 2018). Starvation among nestlings due to a parent's limited foraging success, may be an indirect consequence of harsh rain (Anctil *et al.* 2014). Effects of weather on falcons living in Mediterranean climates is much less known, although they seem basically similar to those in the beforementioned bioclimate zones. Temperature and rainfall emerged as significant correlates with the Peregrine breeding performances in Mediterranean South Africa, and eggs were laid later with increasing precipitation and number of rainy days, while the Lanner Falcon was largely unaffected by environmental variables (Jenkins 2000). In Peregrines of the Australian cool temperate zone, many aspects of breeding performances (timing and duration of egg-laying, clutch size, nest success, breeding density) were negatively influenced by rainfall, so that the total production of the population was lower in the wettest years (Olsen & Olsen 1988, 1989).

Although we do not know the exact causal mechanism underlying the overall effects of winter weather (January-March) and the specific effect of February rainfalls on delaying the onset of Peregrine incubation, we can suggest that heavy rains limit hunting activity and/or prey accessibility to male Peregrines, who during the initial stages of reproduction (courtship, laying and incubation) have the task of delivering prey to the females. This can oblige females to find prey for themselves (MS and LZ unpubl. obs.) and/or to wait until the partner's efforts are successful, in any case extending the period in which females reach the optimal body conditions for reproduction or exposing the eggs to the risk of cooling and predation. We never have had evidence of mortality inside the nests (e.g. eggs or nestlings soaking) induced by heavy rains during the study period. This is probably due to the fact that exposed nests on ledges or platforms are very rare in Sicily and most Peregrine nests are sheltered in small caves and rock crevices, so their contents are protected from heavy rain (own unpubl. obs.).

A similar scenario could explain the delay in the onset of Lanner Falcon incubation in response to general winter weather conditions. However, the lack of specific effects needs further explanation. Traditional agroecosystems are disappearing due to land abandonment and intensification in most of the island habitat of the Lanner Falcon (Sarà 2014). These land use changes affect abundance of resident and wintering prey (e.g. larks, pipits, sparrows) characteristic of open habitats (Sokos *et al.* 2013, Nardelli *et al.* 2015, Brambilla *et al.* 2019, Rete Rurale Nazionale & LIPU 2020). Probably the increase in winter temperature is related to changes in land use in decreasing the profitability of hunting territories and the foraging efficiency of this declining and threatened population (Sarà 2014), thus delaying the period in which Lanner Falcon females reach the optimal body conditions for reproduction and lowering the productivity of the population.

Breeding may be timed to improve foraging conditions and consequently survival prospects for newly independent juveniles (Olsen & George 1993, Jenkins 2000), so later reproduction may track the reproduction of prey that currently constitute the bulk of the trophic niche of these falcons (Bondì *et al.* 2016, Vitale 2019), to match the seasonal peak in food availability. In reality, we lack evidence for this hypothesis, which would predict a concomitant delayed reproduction, triggered by climate, even of the main prey species, and it deserves further study.

In any case, the delay in the breeding season of both falcons that we found in our study is remarkable in context of the range of studies on the effects of climate change on birds, which generally show a large advance in the timing of both migration and reproductive phenology (reviews in Lehikoinen & Sparks 2010, Hällfors *et al.* 2020). Earlier breeding is a common response to climate change, as most birds lay earlier when spring temperatures are higher (Dunn 2004, Visser *et al.* 2009), however, a phenological response to climate change resulting in a delay in breeding is uncommon but not exceptional. In passerines, spring reproductive and migratory phenology may advance or delay in response to climate change depending on the latitude of both wintering and breeding area, nesting site and sexual size dimorphism (e.g. Rubolini *et al.* 2005, Both & te Marvelte 2007, Maggini *et al.* 2020). Some species, like the Black-legged Kittiwake *Rissa tridactyla* and Common Guillemot *Uria aalge*, breeding in the North Sea area, indeed show tendencies towards later reproduction over time (Frederiksen *et al.* 2004). The authors correlated this trend with population size, as progressively later breeding of Black-legged Kittiwakes was associated with low population density (Frederiksen *et al.* 2004). An explanation that could apply to our declining Lanner Falcon population, but not to the stable/increasing Peregrine population. Similar to Peregrines, the incubation onset of Common Eider *Somateria mollissima* is later after wetter and windier winters (Jónsson *et al.* 2009) and that of Mauritius Kestrel *Falco punctatus* in wetter springs (Senapathi *et al.* 2011).

Despite the generally common response of both large falcons to changing climate conditions, some results lead us to emphasize that the Lanner Falcon seems more sensitive than the Peregrine to the chain of effects induced by climate change. For instance, the R^2_{adj} and beta coefficient values, higher in Lanner Falcon than in Peregrine, suggest a stronger effect of the delay in incubation onset on the decrease in productivity of the first species. The most obvious difference is certainly that the quality of Lanner Falcon breeding sites (BQI) is influenced by the overall climatic conditions of the late breeding season and by the specific effects of May precipitation, compared to the Peregrine, whose BQI is not affected by climatic conditions of the early and late breeding seasons. Sudden, heavy rainfall in May, which is increasing, as found using ERA-interim data, is likely to affect offspring survival on parts of the island where Lanner Falcon sites are more exposed to rain or by decreasing parental foraging success. This climate sensitivity of Lanner Falcons' reproductive performance adds to the negative effects of degradation of traditional agricultural ecosystems on the species' occupancy (Sarà 2014). The decline in productivity of both species is worrying; even if the larger population size of Peregrines and its plasticity can better buffer the impact of climate change, there may be dramatic cascading effects on the Lanner Falcons' future survival and persistence on the island.

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SAMENVATTING

Op Sicilië hebben wij de effecten van het weer op de timing en het reproductiesucces van de daar broedende Slechtvalken *Falco peregrinus brookei* en Lannervalken *F. biarmicus feldeggii* onderzocht. In de periode 1979-2019 zijn zowel de gemiddelde voorjaarstemperatuur als de hoeveelheid regenval op Sicilië toegenomen. In dezelfde periode zijn beide valkensoorten ongeveer een week later gaan broeden. Wij vonden dat zowel de omstandigheden gedurende de winter als de eilandregio's en het onderzoekjaar van invloed waren op de datum waarop de valken gingen broeden. De toename van de regenval in februari heeft de datum van broeden bij de Slechtvalk verlaat. Welke factor bij de Lannervalk verantwoordelijk is geweest voor het later broeden kon niet worden vastgesteld. Als gevolg van het later broeden worden er bij beide soorten nu minder jongen per territorium grootgebracht dan voorheen. De weersomstandigheden in het late voorjaar voorspelden de kwaliteit van de broedplaats bij Lannervalken, maar niet bij Slechtvalken. Bij beide valkensoorten zijn de weersomstandigheden op Sicilië van invloed op de broedfenologie, maar de Lannervalk lijkt gevoeliger voor het veranderde klimaat dan de Slechtvalk. De klimaateffecten komen bovenop andere al bestaande antropogene effecten die een negatieve invloed hebben op het voortbestaan van deze, voor Europese begrippen, grote eilandpopulaties.

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SUPPLEMENTARY MATERIAL

Table S1. Result of the Ljung-Box Q test, used to check whether or not climate data over the time-series 1979-2019 are random and independent. Ljung-Box Q tests were run independently for the two climate variables in each ERA-Interim area and per every month considered in the study. The null hypothesis of the Q test is that all the autocorrelations up to lag $k = 1$ are 0; while according to the alternative hypothesis the autocorrelations of one lag differ from 0. All cumulated precipitation and soil temperature but three areas in April had zero first-order autocorrelation. AC = Autocorrelation value, Q = Ljung-Box Q statistics, P = significance value. Climate sectors numbered from north-west to south-east Sicily: 1.north-west, Trapani; 2.mid-north, Palermo; 3.mid-north, Madonie mt.; 4.north-east, Nebrodi mt.; 5.south-west, Trapani; 6.mid-south, Sicani mt.; 7.central, Enna; 8.mid-east, Aetna & Catania; 9.south-east, Gela Plain.

		Cumulated Precipitation			**Soil Temperature**		
	ERA-Interim area	AC	Q	P	AC	Q	P
January	1.north-west, Trapani	–0.066	0.192	0.661	0.017	0.012	0.912
	2.mid-north, Palermo	–0.096	0.403	0.526	0.023	0.023	0.879
	3.mid-north, Madonie mt.	–0.114	0.576	0.448	0.079	0.274	0.601
	4.north-east, Nebrodi mt.	–0.073	0.233	0.629	0.062	0.170	0.680
	5.south-west, Trapani	–0.046	0.095	0.758	–0.042	0.077	0.782
	6.mid-south, Sicani mt.	–0.149	0.977	0.323	–0.050	0.109	0.741
	7.central, Enna	–0.197	1.713	0.191	–0.112	0.551	0.458
	8.mid-east, Aetna & Catania	–0.149	0.976	0.323	–0.276	3.347	0.067
	9.south-east, Gela Plain	–0.279	3.435	0.064	0.064	0.179	0.673
February	1.north-west, Trapani	–0.094	0.388	0.533	0.194	1.661	0.197
	2.mid-north, Palermo	–0.117	0.608	0.435	0.180	1.424	0.233
	3.mid-north, Madonie mt.	–0.203	1.810	0.179	0.207	1.894	0.169
	4.north-east, Nebrodi mt.	0.070	0.217	0.641	0.247	2.700	0.100
	5.south-west, Trapani	–0.093	0.378	0.539	0.137	0.824	0.364
	6.mid-south, Sicani mt.	0.043	0.083	0.773	0.070	0.213	0.645
	7.central, Enna	–0.039	0.067	0.796	0.074	0.242	0.623
	8.mid-east, Aetna & Catania	–0.086	0.322	0.570	0.038	0.063	0.802
	9.south-east, Gela Plain	–0.128	0.727	0.394	0.277	3.373	0.066
March	1.north-west, Trapani	0.044	0.085	0.770	0.209	1.927	0.165
	2.mid-north, Palermo	0.044	0.087	0.769	0.175	1.356	0.244
	3.mid-north, Madonie mt.	0.062	0.167	0.683	0.196	1.685	0.194
	4.north-east, Nebrodi mt.	0.050	0.109	0.742	0.222	2.176	0.140
	5.south-west, Trapani	0.169	1.262	0.261	0.228	2.295	0.130
	6.mid-south, Sicani mt.	0.086	0.327	0.567	0.109	0.520	0.471
	7.central, Enna	0.109	0.522	0.470	0.099	0.436	0.509
	8.mid-east, Aetna & Catania	0.092	0.374	0.541	0.149	0.975	0.323
	9.south-east, Gela Plain	0.094	0.389	0.533	0.245	2.642	0.104
April	1.north-west, Trapani	–0.107	0.501	0.479	0.408	7.346	0.007
	2.mid-north, Palermo	–0.166	1.216	0.270	0.399	7.013	0.008
	3.mid-north, Madonie mt.	–0.112	0.548	0.459	0.399	7.013	0.008
	4.north-east, Nebrodi mt.	0.058	0.151	0.698	0.263	3.042	0.081
	5.south-west, Trapani	–0.186	1.518	0.218	0.272	3.268	0.071
	6.mid-south, Sicani mt.	–0.097	0.413	0.520	0.191	1.614	0.204
	7.central, Enna	–0.005	0.001	0.975	0.145	0.933	0.334
	8.mid-east, Aetna & Catania	0.172	1.299	0.254	0.149	0.983	0.321
	9.south-east, Gela Plain	–0.091	0.368	0.544	0.158	1.100	0.294
May	1.north-west, Trapani	–0.162	1.152	0.283	0.108	0.516	0.473
	2.mid-north, Palermo	–0.111	0.545	0.460	0.139	0.850	0.356
	3.mid-north, Madonie mt.	–0.194	1.661	0.197	0.150	0.996	0.318
	4.north-east, Nebrodi mt.	–0.009	0.003	0.954	0.111	0.546	0.460
	5.south-west, Trapani	0.008	0.003	0.958	0.107	0.508	0.476
	6.mid-south, Sicani mt.	0.107	0.503	0.478	0.097	0.414	0.520
	7.central, Enna	0.022	0.022	0.883	0.069	0.213	0.645
	8.mid-east, Aetna & Catania	–0.060	0.160	0.689	0.004	0.001	0.977
	9.south-east, Gela Plain	–0.113	0.567	0.451	0.018	0.014	0.906

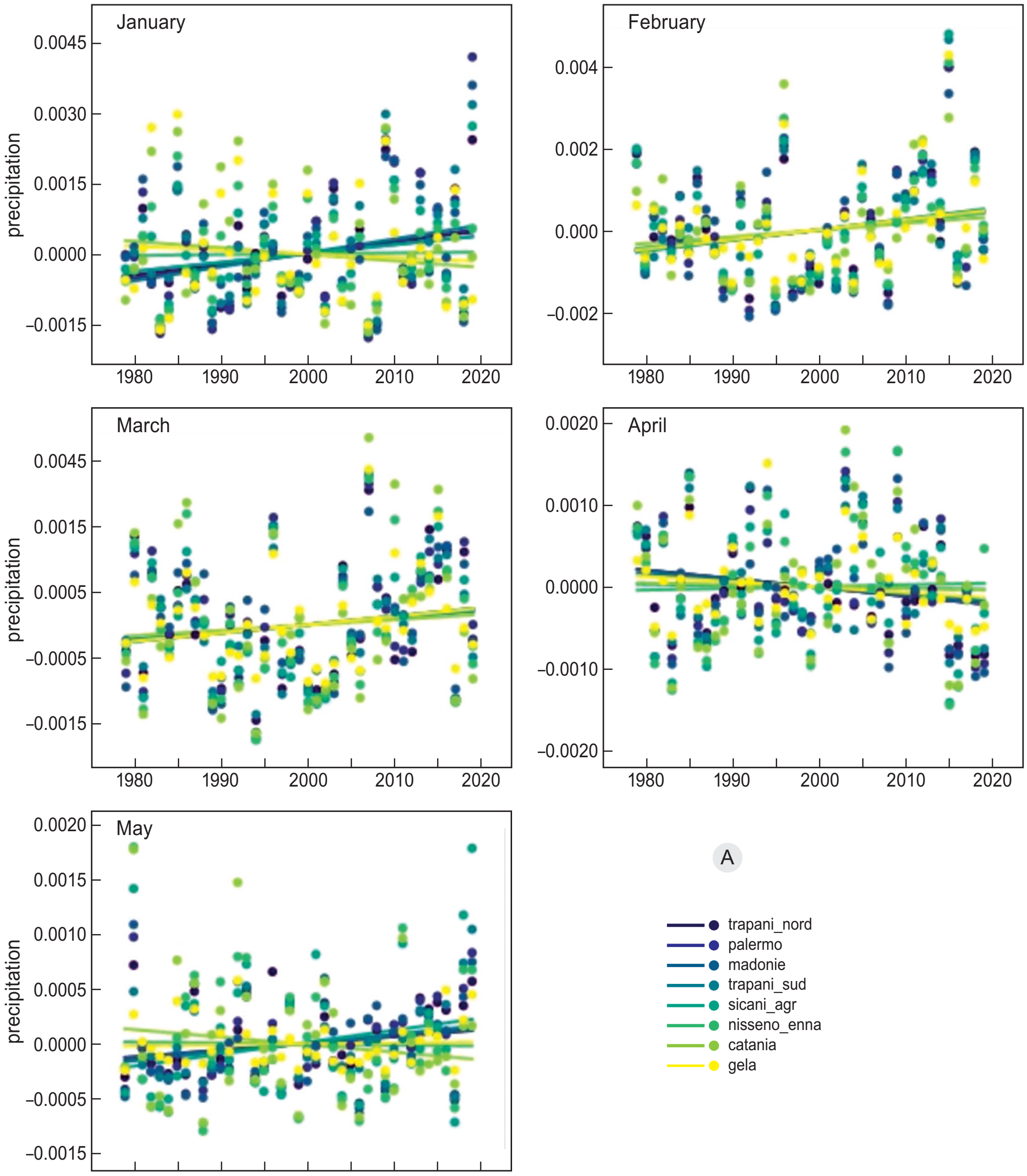

Figure S1. Prais-Winsten Regression, above anomaly of cumulated precipitation, below of soil temperature. Fitted curve is predicted by Prais-Winsten regression coefficients, colour dots show data per every ERA-Interim area corresponding to studied sites of large falcons (Peregrine *F. peregrinus* and Lanner Falcon *F. biarmicus*). Climate sectors numbered from north-west to south-east Sicily: 1.north-west, Trapani; 2.mid-north, Palermo; 3.mid-north, Madonie mt.; 4.north-east, Nebrodi mt.; 5.south-west, Trapani; 6.mid-south, Sicani mt.; 7.central, Enna; 8.mid-east, Aetna & Catania; 9.south-east, Gela Plain.

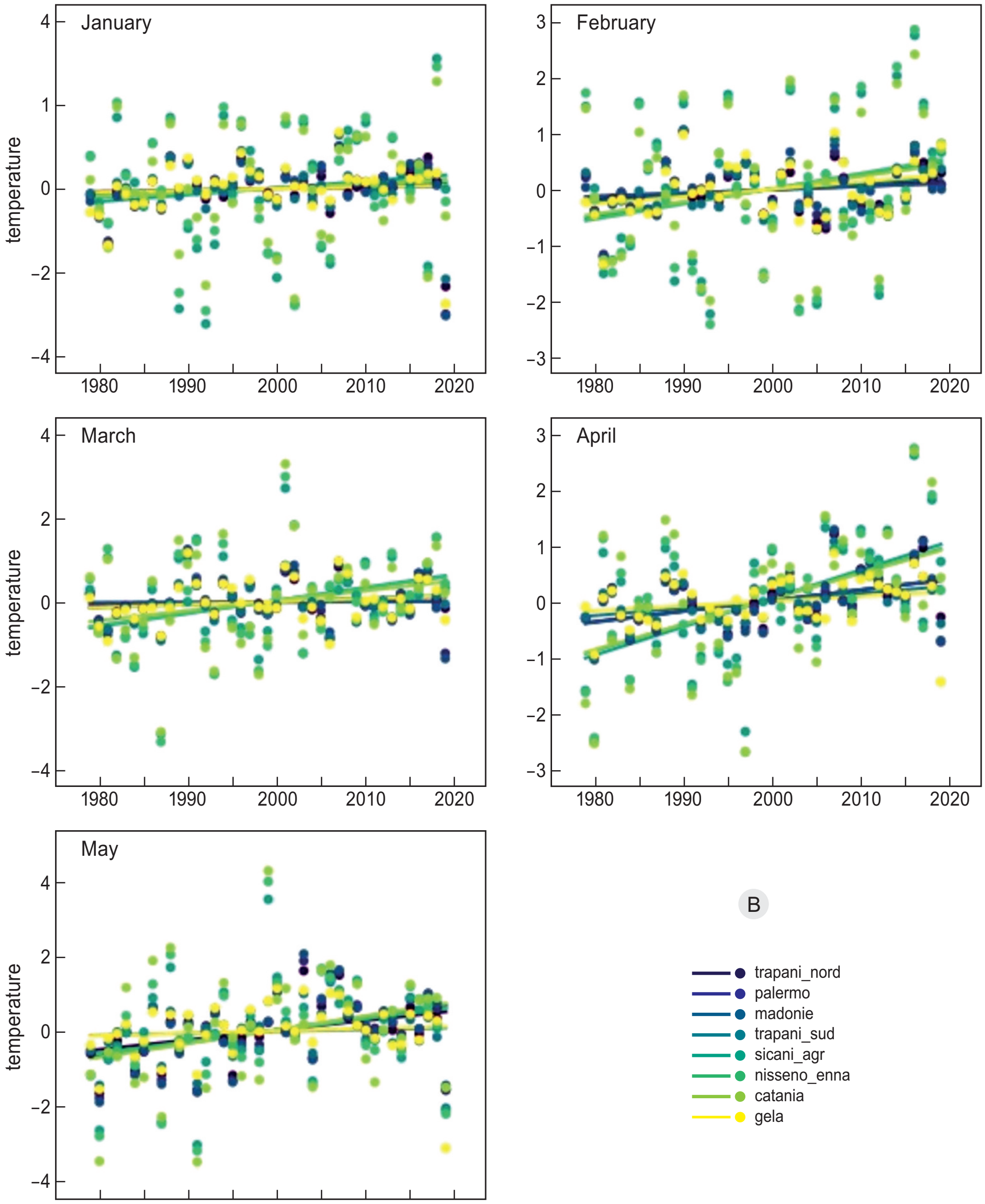

Figure S1. Continued.