Synchronizing biological cycles as key to survival under a scenario of global change: The Common quail (*Coturnix coturnix*) strategy

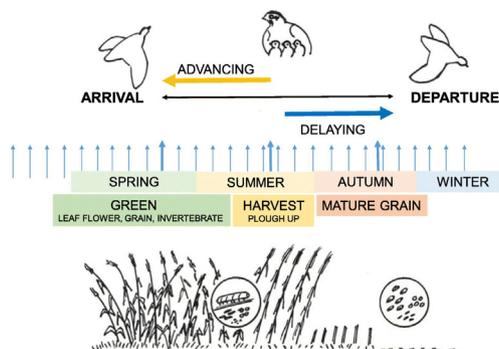Jesús Nadal [a,*], Carolina Ponz [a], Antoni Margalida [a,b]

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HIGHLIGHTS

- The impact of climate warming and farming practices on quail phenology is unknown.
- We use a long-term study (1961-2014) of quail-ringing in Spain and data on variation in rainfall and temperature.
- Our results suggest that increases in temperature and decreases in precipitation modify quail phenology.
- Quail movements and breeding attempts are eco-synchronized sequentially in cloudy regions.
- Quails attempt to overcome the negative impacts by searching for alternative high-quality habitats.

GRAPHICAL ABSTRACT

ABSTRACT

Breeding grounds are key areas for sustaining Common quail (*Coturnix coturnix*) populations as this species is characterised by short life expectancy that requires high offspring production. Annually, breeding quails make up to three breeding attempts in different places. However, the impact of climate warming on quail phenology is unknown. Here, we use a long-term study (1961–2014) of quail-ringing in Spain and data on variation in rainfall and temperature over the past 86 years to evaluate how quails have responded to climate change in recent years. Our aim was to understand how this species is adapting to new farming practices and climate change. Our results suggest that increases in temperature and decreases in precipitation modify quail phenology. In hot years, an advance in mean arrival dates and stay stages but a delay in departure dates was found. However, in rainy years a delay in the mean start of the stay stage occurred. In cloudy areas, our findings show that quails advance their stay periods in hot and dry years and delay them in cold and rainy years. Accordingly, quail movements and breeding attempts are eco-synchronized sequentially in cloudy regions. Our results suggest that quails attempt to overcome the negative impacts of climate change and agricultural intensification by searching for alternative high-quality habitats. This strategy could explain how quail populations maintain viable and sustainable populations despite being legally harvested with regulated hunting.

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1. Introduction

Climate change is a major threat to biodiversity and is provoking greater and accelerating extinction risks (Cahill et al., 2012; Pacifici et al., 2015; Urban, 2015). Species vulnerability is greatly affected by global

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change and in most cases conservation statuses will depend on an organism's adaptive capacity (Langham et al., 2015; Wade et al., 2017). However, the speed of change places a limit on adaptive capacity and biodiversity (Bateman et al., 2016; Boucher-Lalonde et al., 2014; Chen et al., 2011). Breeding and wintering areas are closely linked to the life history of migratory species. Warming favours some populations and species but is handicap for others — depending on their behaviour, physiology, habitats and, in particular, geographical distribution (Hughes, 2000; Marra et al., 2015). Farmland birds and cold habitats are most negatively affected by global change due to the shift to poorer habitat quality (Jørgensen et al., 2016; Rushing et al., 2016). As a result, altered habitats are having a serious impact on species interactions and the structure and function of ecological communities (Blois et al., 2013; Isbell et al., 2015; Savo et al., 2016).

Previous research into the effects of global change on migratory birds have documented, among other factors, how phenology mismatches lead to a desynchronization within biological cycles due to changes in arrival and departure dates (Ge et al., 2015; McDermott and DeGroote, 2016); this will have implications for niches and food availability (Jezkova and Wiens, 2016; Thorup et al., 2017) in both breeding and wintering areas and provoke changes in habitat quality (Ahola et al., 2004; Sanz et al., 2003). Warming affects birds in many ways such as how the photoperiod triggers migration and reproduction since temperature has regulatory effects on both these factors (Jenouvrier, 2013; Singh et al., 2012). Food mismatch is an important ecological problem for bird reproduction as species eco-synchronize the hatching and growth of chicks with abundance peaks in optimal food sources such as plant products, caterpillars, grasshoppers, flies and other invertebrates (Studds and Marra, 2011; Visser and Both, 2005). Arriving earlier and departing later is the most likely adaption to warming employed by summer migrant birds (Jonzén et al., 2007).

The Common quail (*Coturnix coturnix*) is an Afro-Palearctic migratory bird with a broad continental distribution. Certain individuals exhibit sedentary lifestyles, while others are short- or long-distance migrants. Quails inhabit pastures and farmland, and have an intricate life strategy: winter nomadism, spring migration, sequential breeding and autumn migration (Rodriguez et al., 2009). The Western Palearctic population begins breeding (first attempts) in North Africa and southern Spain; second attempts take place mainly in Spain, while third attempts are generally in Spain and Central Europe. As a result, Spain is a key area in the breeding strategy of this quail population and so knowledge of the effects of warming and intensive farming are essential if we are to understand changes occurring in the biology of this and other migratory birds.

Here, we use data from a long-term study (1961–2014) of quail-ringing in Spain and a vast meteorological data set (1930–2015) of variation in rainfall and temperature in Spain over the past 86 years to evaluate how quails are responding to climate change. Our overall aim was to understand how this species is adapting to alterations in farming practices and climate change.

2. Methods

2.1. Ecology of the species

As shown in Fig. 1, climate has the effect of advancing or delaying biological cycles (Gordo et al., 2005; Knudsen et al., 2007; Peñuelas et al., 2002) and so climate change may modify the arrival and departure dates of migratory birds. In some species warming leads to the advancing of the date of arrival and a delay in the date of departure (Cruz-Mcdonnell and Wolf, 2016; Macmynowski et al., 2007). Climate has a direct influence on the ability of quails to find food (abundance of grain and invertebrates) and on the likelihood of predation (cover density), and also affects physiology and behaviour (Gillson et al., 2013; Madliger and Love, 2016). Starvation and predation risk are mutually dependent (Ockendon et al., 2014; Scheffers et al., 2016) and both have an impact on physiology and behaviour (Bulla et al., 2016; Mariette et al., 2015). Survival depends on a balance between starvation and the predation risk, as well as on physiological condition (health) and behavioural responses (experience) to daily challenges (Bonter et al., 2013; Hethcoat and Chalfoun, 2015).

Migratory quail move through different landscapes seasonally, exploiting shifting environmental resources and taking advantage of patches with abundant food (Somveille et al., 2015; Zuckerberg et al., 2016). Quails' annual cycle can be divided into four biological stages: winter, pre-nuptial migration (arrival), breeding stays, and post-nuptial migration (departure); in Spain, arrivals take place in February–April, breeding stays last through May–July and departures occur in August–October. Quails link habitat quality to population demography via movement patterns (Taylor et al., 2016), and initially follow agricultural greenup for breeding but then abandon reproduction sites when cereals are harvested (Fig. 2). Mismatches can occur when components of the biological cycle such as hatching dates and food supply for chicks become desynchronized (Saino et al., 2011).

In earlier research designed to select the variables that most influence and explain the data in the quail-ringing database, agriculture-related variables (dry or irrigated land) were discarded due to their small (non-significant) contribution to the model (logistic regression). However, agrosystems are associated and affected by cloudy areas, defined as geographic areas with similar level of cloud coverage (Appendix Fig. 7).
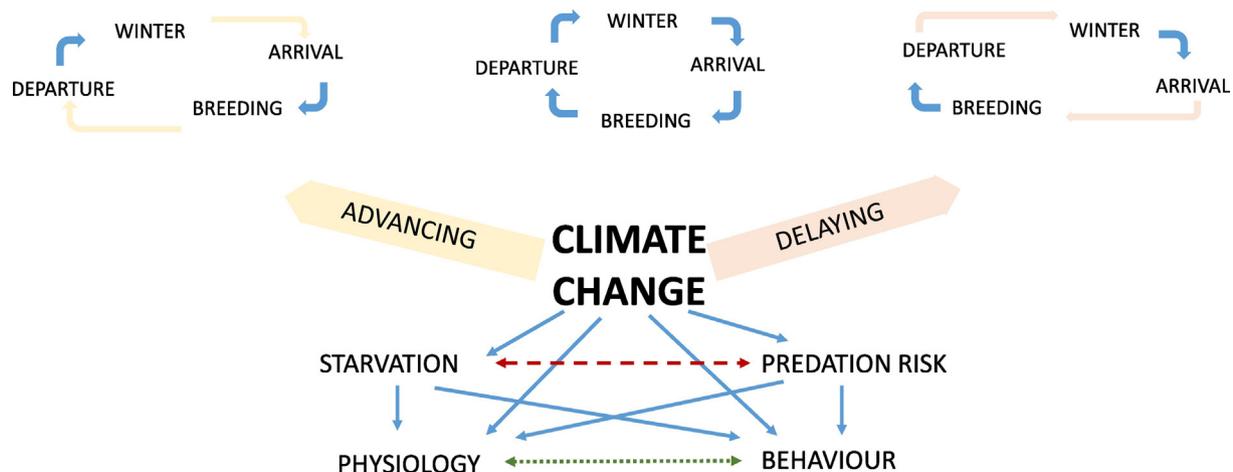

Fig. 1. Hypothetical quail biological cycle framework related to climate effects. Warming causes the advance of dates of spring migration and a delay in autumn return, which in turn modify ecological balances.
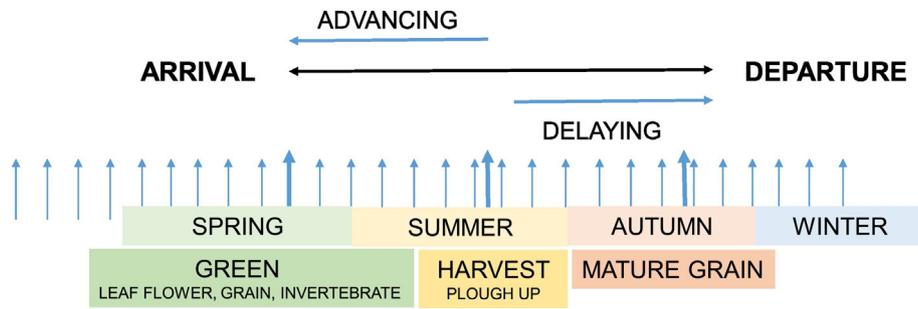
Fig. 2. Synchronization of the biological cycle of quail with plant growth. Advances and delays in quail migration and possible effects on breeding. Vertical arrows are time units (15 days), thick arrows indicate arrival (February–April), stay (May–July) and departure (August–October) quail stages in Spain.

2.2. Data collection

We used quail ringing data consisting of 43,194 records (Table 1) from a number of ringing schemes: 37,706 records from SEO/BirdLife (ICONA rings), 4209 records from hunting associations (FEDENCA rings) and two autonomous communities (Junta de Castilla y León and Cabildo de Tenerife rings), and 1279 records from the Sociedad de Ciencias Aranzadi (ARANZADI rings) covering the period 1961–2014. We filtered and homogenized these datasets to generate standardized information that included Julian date, longitude, latitude and altitude according to Nomenclator (IGN, 2015) of the ringing locality, and habitat (dry land or irrigated land). The temporal and spatial distribution of ringing teams were associated with the presence and abundance of quail in the territory. Given that this study does not attempt to evaluate quail abundance using ringing data and the fact that sample sizes at each stage are important, the differences in ringing effort should not affect our results.

We obtained rainfall and temperature data from AEMET (the Spanish Meteorological Office) consisting of 2,724,261 monthly rainfall records from 10,834 stations, and 1,045,137 average monthly temperature records from 5332 stations. We then built a meteorological database for the eight cloudiest Spanish regions according to the maps in Wilson and Jetz (2016). In each geographic area (cloudy region) and year, we used all the assigned stations to obtain monthly averages for temperature and rainfall, and then calculated the average temperature and rainfall for the three biological stages (arrival: February–April, stay: May–July; departure: August–October; Fig. 2). Finally, we matched the ringing database with the meteorological database and each quail record (i.e. location and date of capture) was assigned the climate data corresponding to the average for the geographic region in that month, stage and year.

2.3. Statistical analyses

We calculated the mean Julian date for each stage (arrival, breeding stay and departure) for Spain and for cloudy areas, as well as monthly and annual mean precipitation, and temperature for each stage in Spain and in geographic areas. Then, for each cloudy area we obtained mean precipitation and temperature figures for each period (arrival: February–April, stay: May–July; departure: August–October). Following the same process, we also calculated the mean Julian ringing date for each geographic area (Canary Islands, Ceuta-Melilla, Centro-Sur, Balearic Islands, North Plateau, North, Duero Valley, Ebro Valley). We built simple regression models with meteorological variables (year and mean) and the Julian date of ringing. We used JMP11 (SAS, 2015) to statistically analyse the studied variables.

3. Results

Over the past 86 years, precipitation in Spain has decreased significantly during the stay stage (May–July) ($R^2 = 0.12$, F = 11.48, P < 0.001, n = 86) but not for arrival (February–April) ($R^2 = 0.01$, F = 0.9, P > 0.35, n = 86) or departure (August–October) periods ($R^2 = 0.002$, F = 0.14, P > 0.75, n = 86 Fig. 3). In the stay stage, with increased precipitation, the mean date of quail ringing was delayed significantly ($R^2 = 0.24$, F = 50.72, P < 0.001, n = 164); however, no relationship was found between increased precipitation and either arrival ($R^2 = 0.002$, F = 0.25, P > 0.62, n = 143) or departure ($R^2 = 0.001$, F = 0.13, P > 0.72, n = 108 Fig. 4).

In the last 86 years, temperatures have increased significantly for arrival ($R^2 = 0.12$, F = 11.25, P < 0.001, n = 86), stay ($R^2 = 0.15$, F = 15.34, P < 0.0002, n = 86) and departure ($R^2 = 0.16$, F = 16.18, P < 0.0001, n = 86) stages. The arrival stage – that is, the mean Julian date of ringing – advanced significantly with increased temperature ($R^2 = 0.25$, F = 45.69, P < 0.001, n = 143); the stay stage – mean Julian date of ringing – advanced in accordance with increases in temperature ($R^2 = 0.35$, F = 86.58, P < 0.0001, n = 164); and the mean Julian date of ringing for the departure stage was delayed significantly with increases in temperature ($R^2 = 0.23$, F = 30.69, P < 0.0001, n = 108 Figs. 5 and 6, Table 2).

4. Discussion

Our results confirm an increase in temperatures in Spain in three stages of quail life histories: arrival (February–April), stay (May–July) and departure (August–October), as well as a decrease in precipitation during the stay stage. By contrast, no significant differences were found in precipitation trends in relation to arrival and departure stages (Gordo and Sanz, 2010; Saino and Ambrosini, 2008). These findings are consistent with other warming indicators such as those of the climatic panel (IPCC, 2014), Northern Hemisphere ice sheets (Zhang et al., 2014), faster warming rates in recent years (Hausfather et al., 2017), the Agulhas current (Beal and Elipot, 2016), greenhouse gases (Snyder, 2016) and rainfall regimes in the Sahara (Tierney et al., 2017).

Our findings also agree with previous studies that indicate the earlier arrival of migratory birds on breeding grounds (Kullberg et al., 2015) and later departure dates (Rivalan et al., 2007). In warm years, quails advanced their mean arrival and stay dates, and delayed their departures. This is consistent with the findings of delays in mean dates of stay during rainy years. Advances and delays of dates in stages of biological cycle can be interpreted as quails' responses to thermal cues that enable them to adapt their biological cycle to habitat phenology (Both and

Table 1
Quail banded in Spain according to ringing organization and ring type.

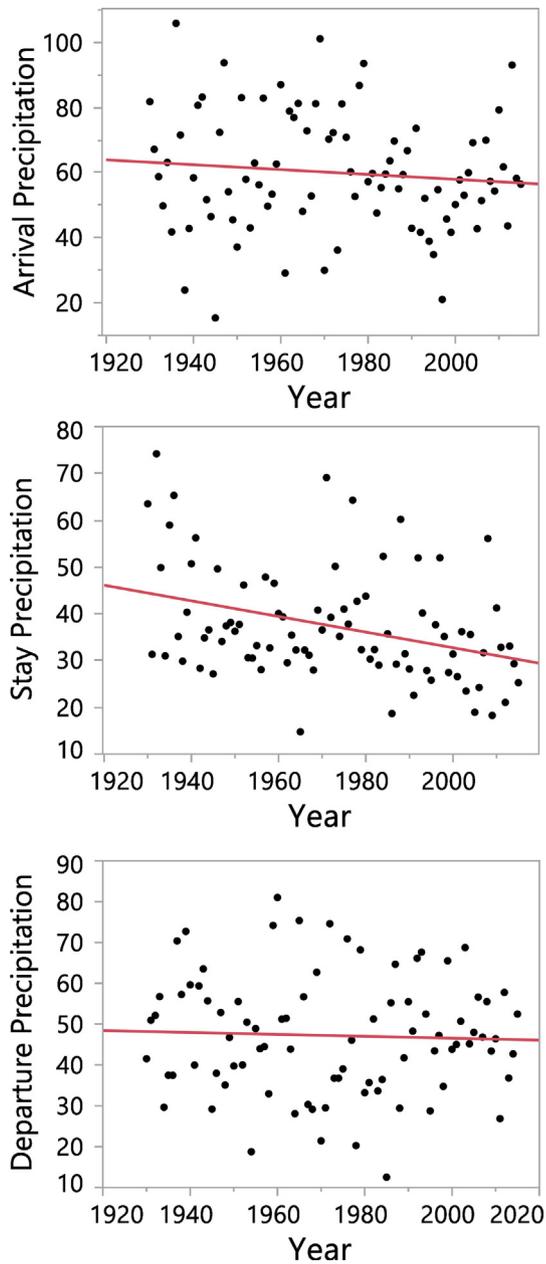| Ring type	Period	N years	N quail banded	Rings/years
SEO-ICONA	1961–2014	39	37,706	967
ARANZADI	2000–2014	15	1279	85
FEDENCA-CA	2002–2014	13	4209	324
Total	1961–2014	39	43,194	1108

Fig. 3. Variation in mean monthly precipitation (mm) for arrival (February–April), stay (May–July) and departure (August–October) dates in Spain during the period 1930–2015.
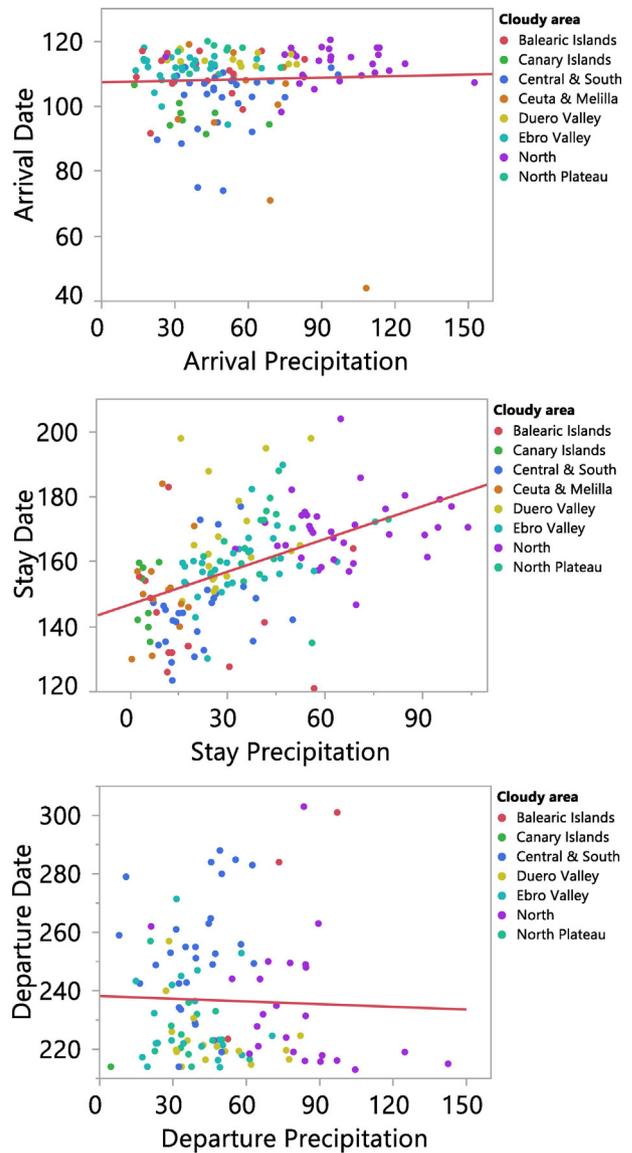

Fig. 4. Variation in mean the Julian date of quail ringing for arrival (February–April), stay (May–July) and departure (August–October) in Spain in relation to mean stage precipitation (mm). Colours show the different populations studied. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Visser, 2005). In this sense, many species of migratory birds face the problem of how to disengage their annual cycles from habitat cycles. Mismatches with habitat can lead to trophic-, cover-, mimetic- and eco-synchrony-related problems (Wiens et al., 2009; Ockendon et al., 2013). Accordingly, thermal delay has been suggested as one of the main drivers of population decline (Saino et al., 2011). On the other hand, thermal stress has been proposed as an important constraint on the use of space and survival rates (Tanner et al., 2017).

Thus, the study of long-term data series is key in understanding trends in global changes in biology (Conklin et al., 2010; Stephens et al., 2016). Long-term data series can also help understand stages of biological cycles. The ability of species to respond to new habitat conditions and their capacity to adjust will determine their vulnerability and their distribution limits (Goodenough and Hart, 2013; Moss et al., 2010). In particular, migration is an adaptive response to geographical and seasonal variation in resources (Small-Lorenz et al., 2013). Quail life strategies are characterised by sequential breeding and nomadic movements,

with females requiring 50 days for each breeding attempt; afterwards, they disperse in search of similar quality breeding habitat. We found that breeding stays and subsequent movements vary with precipitation and temperature in different geographic areas.

The data gathered for arrival, stay and departure stages suggest that precipitation and temperature have different impacts, although we found a negative relationship between precipitation and temperature that seems to vary with stages (Clement et al., 2016). During the stay stage (May–July), we found contrasting trends in precipitation and temperature (Miller-Rushing et al., 2008). For example, in warm and dry years, quails seem to advance stage dates to coincide with greenup and cereal maturation, while in cold and rainy years quails delay stage dates to eco-synchronize their breeding cycle with the ripening of herbaceous plants (Alexander et al., 2016). Habitat suitability changes with plant cycles and so quails occupy cloudy areas in sequential order in accordance with plant maturation over space and time. Quail follow a green wave of herbaceous plants (Sardà-Palomera et al., 2012), although irrigated land with alfalfa, fodder and maize can also provide continuously green habitat for quails, albeit with limitations imposed

Table 2
Slopes from regression of rain and temperature with year, and with quail average dates ± SD. Significant values in bold. Arrival: February–April; stay: May–July; departure: August–October.

Regression with year	b ± SD	Regression with quail date	b ± SD
Arrival precipitation and years	−0.07 ± 0.08	Arrival precipitation and quail arrival date	0.02 ± 0.03
Stay precipitation and years	**−0.17 ± 0.05**	Stay precipitation and quail stay date	**0.34 ± 0.05**
Departure precipitation and years	−0.02 ± 0.06	Departure precipitation and quail departure date	−0.03 ± 0.09
Arrival temperature and years	**0.01 ± 0.004**	Arrival temperature and quail arrival date	**−2.02 ± 0.30**
Stay temperature and years	**0.02 ± 0.004**	Stay temperature and quail stay date	**−4.29 ± 0.46**
Departure temperature and years	**0.01 ± 0.003**	Departure temperature and quail departure date	**4.66 ± 0.84**

by short cut cycles and the use of pesticides (Sax et al., 2013). Quails adapt to warm and cold years by modifying their sequential breeding patterns. Nevertheless, further research is still needed to better understand their capacity to adjust to major changes (Schaefer et al., 2008).

Land use limits the availability of suitable habitat for quails, while the likelihood of successful breeding is associated with cloudy areas and plant ripening. Quails have to synchronize their breeding attempts with plant cycles but also have to find a balance between starvation and predation risks, as well as their migration routes with resources and suitable climate. Temperature and greenness seem to be the most likely cues that indicate the suitability of a place and time for breeding (La Sorte and Fink, 2017). Conspecific and heterospecific interactions regulate reproduction opportunities, and there is evidence that migration
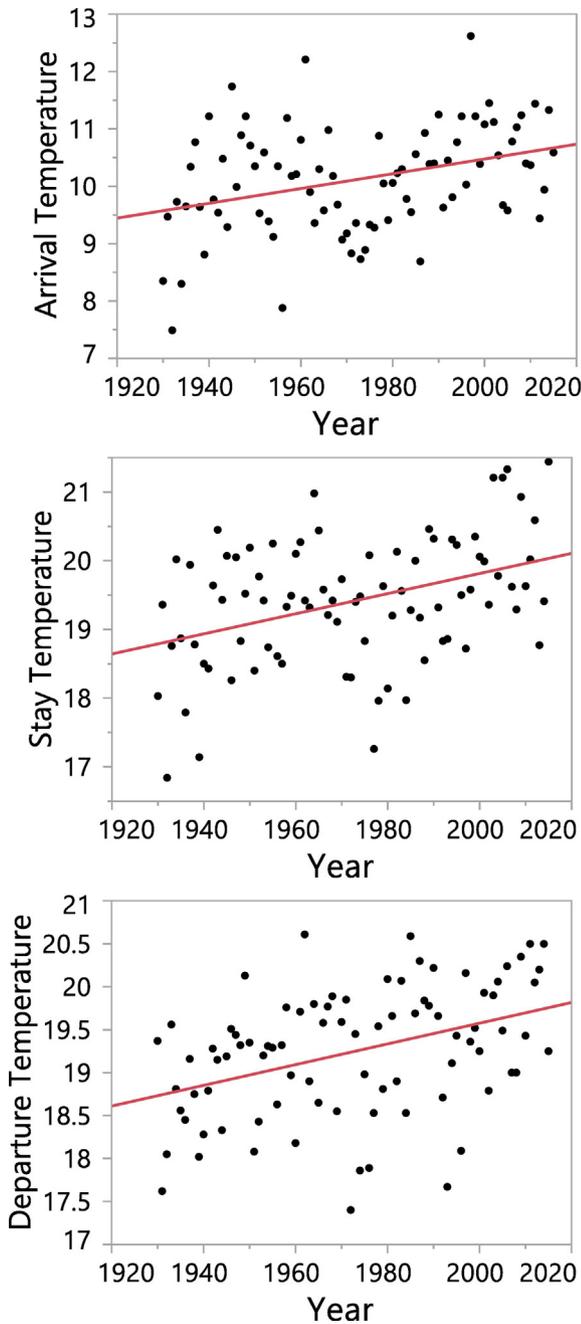

Fig. 5. Variation in mean monthly temperature (°C) for arrival (February–April), stay (May–July) and departure (August–October) dates in Spain in relation to years during the period 1930–2015.
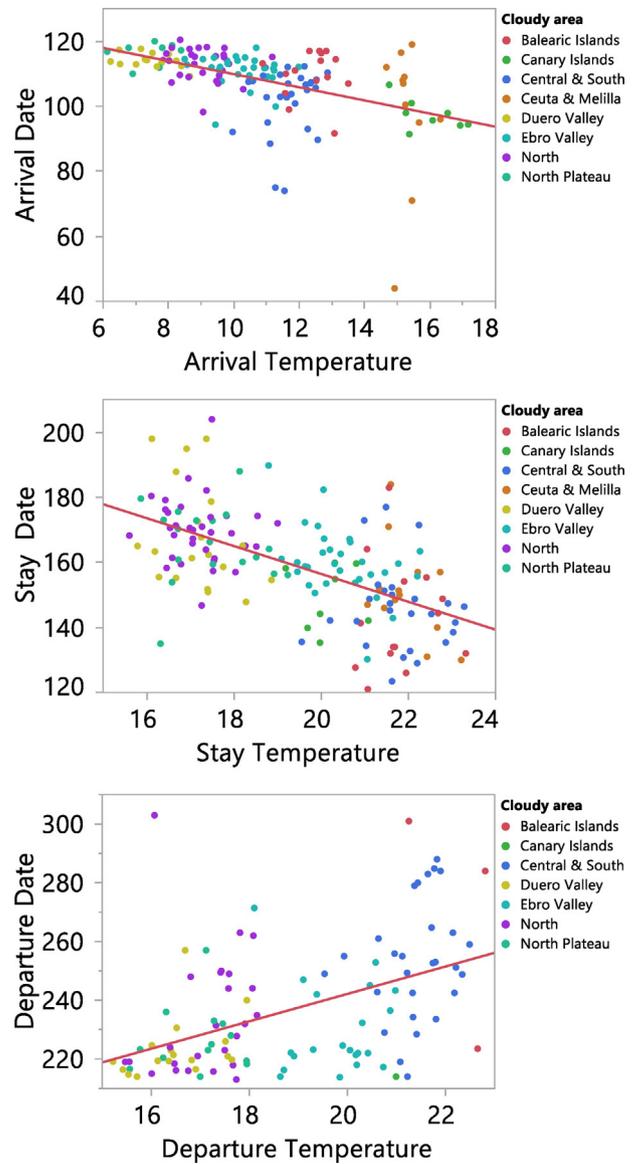

Fig. 6. Variation in the mean Julian date of quail ringing for arrival (February–April), stay (May–July) and departure (August–October) dates in Spain in relation to mean stage temperatures (°C).

and nomadism are strategies that maximize the probability of finding a mate and avoiding being misled (Martin and Maron, 2012). Warming and intensive farming reduce the chance of survival and successful breeding. Migratory species with more northerly ranges (polar or near the poles) do not have alternatives to their micro-refuges in the same range, and thus their populations are in decline (Lehikoinen and Virkkala, 2016). Physiological adaptation processes in the past took place over thousands of years, as did changes in geographical habitat. Thus, from a management and conservation perspective, we must mitigate warming and protect micro-refuges. Conserving, recovering and building quality habitats should be a top priority in tasks aimed at protecting migratory bird species.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2017.09.168.

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