



Time, geography and weather provide insights into the ecological strategy of a migrant species

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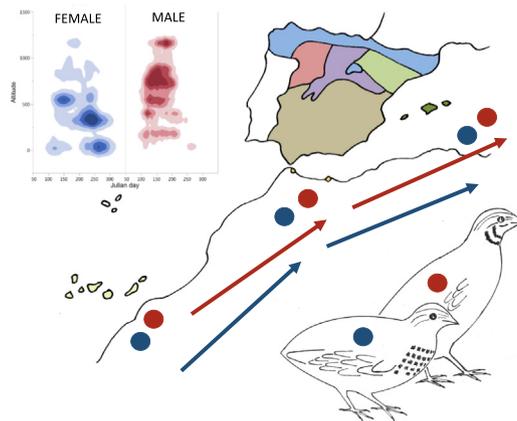
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HIGHLIGHTS

- Afro-palaearctic migratory birds can subsist to global change effects.
- Migration and nomadism timely distribute groups of age and sex in suitable habitats.
- The distribution of quail age and sex class follows variations in weather and habitat suitability.
- The migration added to nomadism is consistent with success in finding optimal habitats.
- Temporal, spatial, age and sex distributions facilitate offset mortality.

GRAPHICAL ABSTRACT



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ABSTRACT

Farmland and migratory bird populations are in decline. The Common quail (*Coturnix coturnix*) provides an exception to this trend and its populations have remained stable over the last two decades. However, some basic facts regarding quail biology and ecology, such as the geographic distribution of age and sex classes during the summer, remain poorly understood. We analyzed 43,194 Spanish quail ringing records from 1961 to 2014 to assess the effects of geography and weather conditions on the probability that individuals will be ringed during the various stages of their annual cycle (arrival –spring migration–, stationary breeding period, departure –autumn migration– and winter) for the different quail age-sex classes over time. We found that spatial distribution of the age and sex classes can be explained by date, latitude, longitude, altitude, rainfall, and temperature. Our results suggest that date accounts for most of the variation in the distribution of quail age classes, followed by the weather variables, and then latitude, and altitude. Similarly, date also accounts for most of the variation in the distribution of the two sexes. These results could partially explain why this species has avoided population decline, since its ecological strategy is based on its temporal and spatial distribution combined with the segregation of age and sex groups. We hypothesize that the distribution of quail age and sex classes follows variations in weather and habitat suitability to exploit seasonal and geographic variations in resource availability. The migratory and nomadic movements of quail, combined with the occurrence of multiple breeding attempts within a single season, may also allow these birds to overcome the impacts of predators and anthropogenic environmental

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change. Conservation and management efforts should therefore take account of these age and sex related temporal and spatial patterns.

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1. Introduction

Migratory birds are excellent quality environment detectors for the continents inhabiting. The migrating birds are therefore a valuable sensor of the environment on earth. The majority of European farmland birds, including Afro-Paleartic migrant species have suffered marked population declines over the last four decades. Agricultural expansion and intensification are responsible for farmland bird declines due to habitat loss and degradation (Bairlein 2016; Pe'er et al. 2014; Taylor et al. 2016; Vickery et al. 2014). Migratory species, especially long-distance migrants, are in decline due to land use, illegal killing and climate warming, provoking phenological mismatch and increasing the risk of natural and non natural mortality factors (e.g. predation, collision with infrastructures, light and acoustic contamination, and pesticide use) (Both et al. 2007; Butler et al. 2010; Cabrera-Cruz et al. 2018; Donald et al. 2006; Gilroy et al. 2016; Goodenough and Hart 2013). However, the Atlantic Common quail (*Coturnix coturnix*) stands in stark contrast to this trend and its numbers have remained stable over the last two decades (Puigcerver et al. 2012). The reasons for this are not fully known but Brown and Taylor (2015) and Rushing et al. (2017) have been speculated to play a role the spatial and temporal use of resources by age and sex groups.

The relationship between life history and population dynamics in migrant species has received little attention and remains largely unclear (Cottee-Jones et al. 2016; Knudsen et al. 2011, but see: Barshep et al. 2017; Rushing et al. 2017). Models explaining the ecology of migrant birds are important tools for management and population conservation (Aloni et al. 2017; Dias et al. 2017; Flack et al. 2016; Marfil-Daza et al. 2013; Somveille et al. 2018). Global changes in climate and environment affect ecosystems and alter the course of biological cycles, making it necessary to understand how different age-sex groups distribute themselves in response to changes in resource availability (Hewson et al. 2016; Lehtikoinen et al. 2016; Luzardo et al. 2014; Nadal et al. 2018a; Saino et al. 2011; Wikelski and Tertitski 2016). Migration theory predicts that travel speed should be balanced with energy savings in terms of fuel accumulation (at stopover sites), and flight type and distance due to constraints such as food acquisition and risk of predation (Alerstam and Hedenstrom 1998; Hedenström 2006, 2008). It provides mechanistic models to explain migration in biophysical as well as in molecular and physiological terms (Cornelius et al. 2012; Gómez et al. 2017) and individual movements have been tracked using geolocators, satellites and GPS technology (Kassara et al. 2017; Procházka et al. 2017).

Some species may have sedentary and migratory individuals according to their geographical range. Within a population, individuals can be either totally or partially migratory. For example, one individual can select different routes in spring or autumn migration choosing benefits (resources for breeding or wintering) with reduced costs (mortality risk) (Gilg and Yoccoz 2010; Horton et al. 2016; Ruiz-Gutierrez et al. 2016; Vardanis et al. 2011). Migratory species move seasonally across different landscapes to exploit changes in natural resources and to find patches where food is most abundant (Rivas Casado et al. 2014; Zuckerberg et al. 2016), hence linking habitat quality and population structure in the process (Newton 2004; Taylor et al. 2016). In the case of quail, depending on latitude and local biogeographical characteristics, populations can be either migrants, partial migrants or sedentary (Fontoura et al. 2000; Mur 2009). During their spring migration, quail travel from the Sahel (the area just south of the Sahara) to the Mediterranean region to start their first breeding attempt. After their arrival there, quail make longitudinal, latitudinal and altitudinal nomadic

movements to find suitable breeding sites, following the 'green wave' (the spring peak of net primary production) (Rodríguez-Teijeiro et al. 2009; Van Der Graaf et al., 2006). They may also make second and third breeding attempts, further north and east in southern and central Europe. Breeding localities and dates vary greatly according to local weather, agrosystem characteristics and the migration route followed. Quail brood their chicks at the same time the plants and invertebrates grow, and abandon their breeding sites after crops ripen and harvest begins. To understand the migratory and nomadic patterns of quail, we examined ringing data from the Spanish breeding grounds (Carboneras et al. 2013; Schmaltz et al. 2015). Several parts of the Iberian Peninsula are home to sedentary and migratory quail populations, and some offer excellent habitats for first, second and third breeding attempts.

Knowledge of the spatio-temporal changes in age and sex distributions of this species may be crucial for improving management and conservation measures. We hypothesized that spatio-temporal changes in age and sex distributions result from alternating bouts of dispersion and aggregation enabling quail to avoid predation and ensure reproduction (Alves et al. 2013; Gow and Wiebe 2014; Rushing et al. 2016). We analyzed several long-term Spanish quail ringing datasets (from 1961 to 2014) to relate age and sex distributions to temporal, geographical and meteorological variables. Our main objective was to build age and sex models in relation to the date, latitude, longitude, altitude and weather for understanding age and sex distribution (Brown and Taylor 2015; Møller 2007; Morrison et al. 2010; Nadal et al. 2018b; Perez et al. 2016). Population structure is important not only for understanding species' dynamics, but can also help to improve the efficiency of conservation efforts by providing the keys to have the greatest effect in sustaining populations. For example determining the space, time, and weather associated with movement and stationary patterns (Duijns et al. 2015; Kölzsch et al. 2016; La Sorte and Fink 2016; Møller et al. 2008). Here, our goals are to interpret the effects of time, geographical distribution and weather conditions on the segregation and aggregation patterns of quail age-sex groups, since the ringing date could provide information on the patterns of their movement and stationary stages.

2. Material and methods

2.1. The study species

The annual cycle of quail can be divided into four stages: 1) wintering (December–February); 2) arrival, spring migration (March–May); 3) stay, stationary breeding period (June–August); and 4) departure, autumn migration (September–November) (Newton 2006a). During the arrival, stationary, and departure stages, quail alternate breeding activity with erratic movements. Their first breeding attempts are in North Africa and southern Spain, followed by second and third breeding attempts in Spain and central Europe. Sequential breeding can include changes in locality, each time at increased latitude or altitude, or movements onto irrigated land. After the peak of breeding, quail begin the departure stage, and commence their post-nuptial migration to return to their African wintering grounds (Newton 2006b) (see Fig. 1).

2.2. Data collection

We obtained 43,194 historic quail ringing records from several Spanish ringing organizations, all relating to the period from 1961 to 2014. The dataset contains 24,174 adults and 13,616 young, being 1267 females and 41,511 males. This included: 37,706 records from SEO/BirdLife: <https://www.seo.org>; 4209 records from hunters'

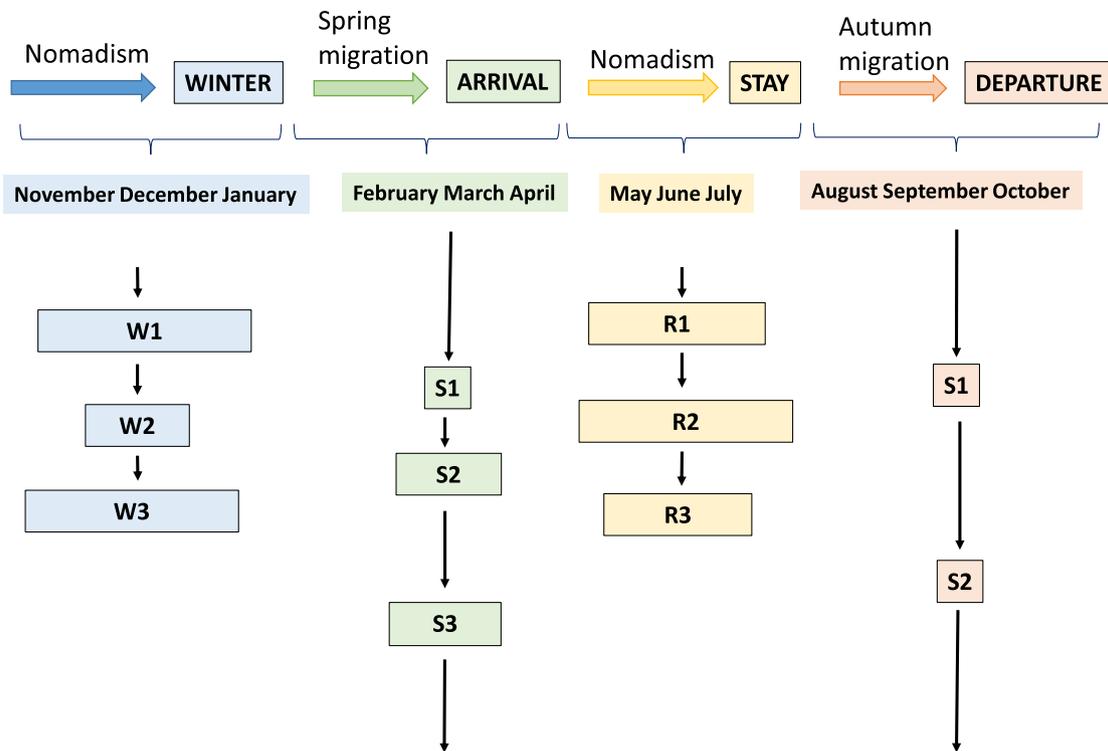


Fig. 1. Hypothetical movements (arrows) and migration stages (boxes) in the quail annual cycle. Winter sub-stages: W1, W2, W3. Stopovers: S1, S2, S3. Reproductive sub-stages: R1, R2, R3. The sizes of the arrows and boxes indicate the duration of the movement between stages and the length of stay in each stage.

associations (FEDENCA: <https://www.fecaza.com/fedenca.html>, FCCL: <http://fedecazacyl.es>) and regional governments (Cabildo de Tenerife: <http://www.tenerife.es/portalcabtfe/es/>); and 1279 records from the Sociedad de Ciencias Aranzadi (ARANZADI: <http://www.aranzadi.es/category/ornitologia>). We filtered and homogenized these three distinct datasets to extract information on the same variables: Julian date, latitude, longitude, altitude, age (adult, individuals more than six months old; young, individuals less than six months old) and sex. The quail information provided in these datasets were mainly captured during the daylight hours using horizontal nets and a female lure. From 2009, several ringing teams also worked during night hours with vertical nets and male and female lures. The large number of records and the model analysis override any bias due to sampling because we always used as much data as possible for age and sex independently in each studied model. Density models are related to each age or sex group and, consequently these are not affected by differences in the number of group data. The temporal, latitudinal, longitudinal, and altitudinal distribution of banding stations were related to the presence and abundance of quail in the area concerned. We assumed that ringing probability was mainly associated with quail ecology. The Spanish quail ringing databases contains more arrival and stay records than departures and winter stays, although as mentioned by other authors (La Sorte and Jetz 2010; Horton et al. 2016), this should not significantly affect our analyses. For logistic regression models unbalanced data affects only the estimate, biasing the predicted probabilities and predictions. We studied differences in the age and sex models to understand the migratory and nomadic movements, dispersion and aggregation explained by date, geographical area and weather.

We obtained rainfall and temperature data from the Spanish Office of Meteorology (AEMET: <http://www.aemet.es/es/portada>) consisting of 2,724,261 monthly rainfall records from 10,834 weather stations, and 1,045,137 average monthly temperature records from 5332 weather stations. Then we built a meteorological database for the eight cloudiest Spanish regions according to Wilson and Jetz (2016) (see Fig. 2). We calculated the average temperature and rainfall for

the four stages (winter, arrival, stay and departure, Fig. 1) in each geographic region and year. We then fitted the entire ringing database to the meteorological database. This procedure associates each bird registry with a geographic area to build models that explain the ecology of the species. A previous work has shown that minimum and maximum rainfall and temperatures may, in some cases, be better predictors of population dynamics than simple averages (e.g., Woodworth et al. 2017), however we search for differences in the age and sex models and not models to explain population fluctuations.

2.3. Statistical analysis

To assess the potential for age- and sex-based structure in the geographic and temporal distribution of common quail, we constructed models in which the number of quail according to the links between age and sex classes and their spatio-temporal distribution to examine the patterns apparent in the data. We calculated logistic regressions of quail age (juvenile/adult) and sex (male/female) on Julian date of capture, latitude, altitude, rainfall at arrival, temperature at arrival, rainfall during the breeding season, temperature during the breeding season, rainfall at departure, temperature at departure, winter rainfall, and winter temperature. We used a backwards stepwise model selection process in which the most parsimonious model was derived by systematically removing potential explanatory variables from the full model described above where additional factors no longer contributed to statistical significance, and calculated the parameter estimates and their standard deviations. The number of factors and the dataset ($N > 37,790$) were always balanced. The AICc (corrected Akaike information criterion), delta AICc and the Akaike weights were used to model selection (Burnham and Anderson 2002). We compared the relative merits (contributions of predictors) of each model with respect to the other models. We performed logistic regression of binary dependent age (adult/young) or sex (female/male), to predict the probability of these outcomes. This probability is a linear combination of independent factors: time, latitude, longitude, altitude and weather (rainfall or

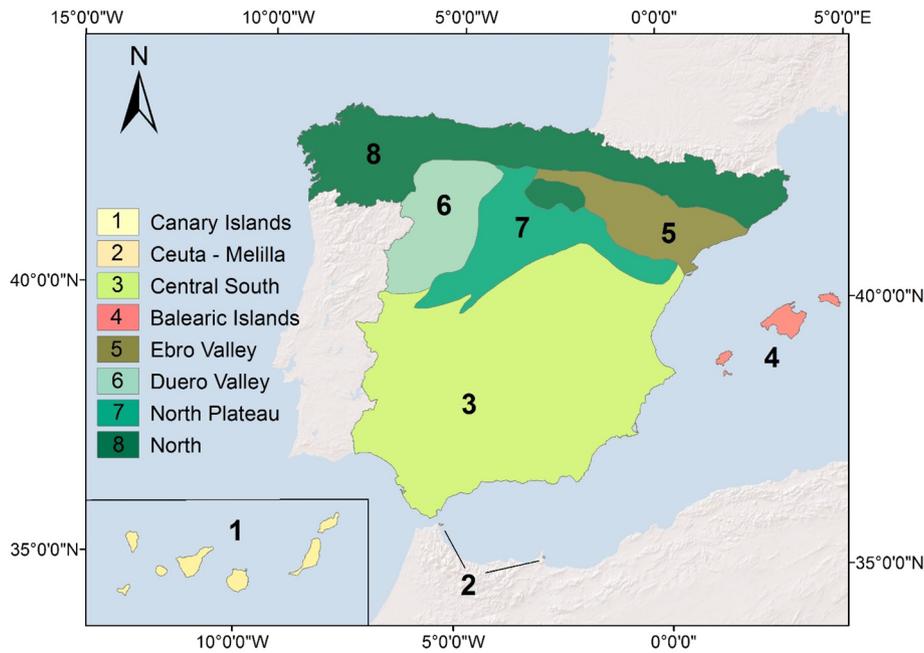


Fig. 2. Distribution of cloudy areas in Spain according to images by Wilson and Jetz (2016): 1 Canary Islands, 2 Ceuta and Melilla, 3 Central South, 4 Ebro Valley, 5 Balearic Islands, 6 Duero Valley, 7 North Plateau, 8 North. The map was created using Arcgis.

temperature over arrival, stay, departure and winter). Obviously rainfall and temperature, and whose stages (arrival, stay, departure and winter) are related, thus rainfall and temperature averages are less limiting than extreme values. We searched for models that can explain the quail presence from the species ecology. We chose a priori the complete model, after reducing the number of predictors. We hoped to find some related ecological keys when interpreting the models of different predictors, because quails are absent from many places which have suitable habitats. We created density graphs (using Graph Builder Intel®) to represent the age-date and sex-date distributions according to latitude and altitude. Statistical analyses were performed using JMP13 (SAS 2015).

3. Results

In the age models, the explanatory variables were ranked in the order of relative importance as follows: date, rainfall at departure, temperature at arrival, latitude, altitude, winter rainfall, winter temperature, rainfall during the stay, rainfall at arrival, and sex (Tables 1 and 2, Supplementary 1 and 2). When we reduced the number of explanatory variables in the models, the order of relative importance was date, latitude and the weather variables. Similar results were obtained for the sex models, the order of relative importance being: date, altitude, latitude, winter temperature, rainfall during the stay, temperature at

Table 1

Models regarding age and sex. The explanatory variables in logistic regressions for Julian date, latitude, altitude, rainfall at arrival (Arrival R), temperature at arrival (Arrival T), rainfall during the stay (Stay R), temperature during the stay (Stay T), rainfall at departure (Departure R), temperature at departure (Departure T), winter rainfall (Winter R), winter temperature (Winter T), age or sex, are ranked in order of relative importance. Average parameter estimates ± standard error (SE shown below) for the explanatory variables in five models to explain the number of ringed quail according to age, and five models according to sex. The standard error is shown in bold for non-significant estimates.

Models		Explanatory variables									
Age	Date	Departure R	Arrival T	Latitude	Altitude	Winter R	Stay R	Winter T	Arrival R	Sex	
A	-0.033 0.001	0.0012 0.0000	0.024 0.002	0.121 0.011	-0.0005 0.0000	-0.0004 0.0000	-0.0006 0.0001	0.009 0.002	0.0004 0.0000	0.184 0.042	
B	-0.033 0.001	0.0012 0.0000	0.024 0.002	0.122 0.011	-0.0005 0.0000	-0.0004 0.0000	-0.0006 0.0001	0.009 0.002	0.0004 0.0000		
C	-0.033 0.001	0.0012 0.0000	0.024 0.002	0.135 0.011	-0.0005 0.0000	-0.0003 0.0000	-0.0005 0.0001	0.007 0.002			
D	-0.033 0.001	0.0011 0.0000	0.018 0.001	0.155 0.009	-0.0005 0.0000	-0.0004 0.0000	-0.0005 0.0001				
E	-0.033 0.001	0.0010 0.0000	0.014 0.001	0.130 0.008	-0.0005 0.0000	-0.0004 0.0000					
Sex	Date	Altitude	Latitude	Winter T	Stay R	Arrival T	Departure R	Arrival R	Stay T	Stay R	Age
A	-0.029 0.001	-0.002 0.000	0.219 0.001	0.022 0.005	-0.001 0.000	0.017 0.005	-0.0005 0.0002	-0.0004 0.0002	-0.009 0.004	0.0002 0.0002	0.016 0.039
B	-0.025 0.001	-0.001 0.000	0.254 0.028	0.022 0.005	-0.001 0.000	0.015 0.005	-0.0005 0.0002	-0.0009 0.0002	-0.007 0.004	0.0000 0.0001	
C	-0.025 0.001	-0.001 0.000	0.254 0.028	0.023 0.004	-0.001 0.000	0.007 0.004	-0.0005 0.0002	-0.0008 0.0002	-0.007 0.004		
D	-0.025 0.001	-0.001 0.000	0.241 0.027	0.022 0.004	-0.001 0.000	0.015 0.005	-0.0005 0.0002	-0.0008 0.0002			
E	-0.025 0.001	-0.001 0.000	0.237 0.028	0.018 0.004	-0.001 0.000	0.021 0.004					

Table 2

Comparison of logistic regressions models linking the number of ringed quail according to age or sex, with the corrected Akaike information criterion (AICc), delta AICc (Δ), weight AICc (W), number of records (N), and the number of parameters with a significant effect (K) ($P < 0.001$).

Models	AICc	Δ	W	N	K
Age					
A	40,275	0	0.99975	37,790	11
B	40,292	16.6	0.0002	37,790	10
C	40,317	41.8	0	37,790	9
D	40,332	56.8	0	37,790	8
E	40,356	81.2	0	37,790	7
F	40,448	172.6	0	37,790	6
G	40,562	286.6	0	37,790	5
H	40,625	349.6	0	37,790	4
I	40,712	436.7	0	37,790	3
J	40,806	531.3	0	37,790	2
Sex					
A	7115	0	1	37,790	11
B	8676	1561.0	0	37,790	10
C	8674	1559.1	0	37,790	9
D	8676	1560.5	0	37,790	8
E	8680	1564.9	0	37,790	7
F	8695	1579.9	0	37,790	6
G	8708	1592.4	0	37,790	5
H	8768	1652.9	0	37,790	4
I	8811	1695.8	0	37,790	3
J	8891	1775.3	0	37,790	2

arrival, rainfall at departure, temperature during the stay, rainfall at arrival, winter rainfall, and age. When the number of predictors was reduced, the order of relative importance was: date, latitude, and altitude followed by the weather variables. For both the age and sex models, the most important factors were the date of capture followed by the latitude or altitude.

The ringing records for the different quail age classes at the same latitude show that adults were ringed on average one month earlier than juveniles (see Fig. 3) adults are on the left and denser (darker) area implicates that arrive before young. On early dates, greater numbers of ringed males were found compared to females, at all altitudes (see Fig. 4 and Table 3) males are on the right and denser (darker) areas at higher altitude implicates that arrive before females.

The weather variables fluctuated within the different stages (arrival, stay, departure and winter, see Figs. 5 and 6). In addition, both average

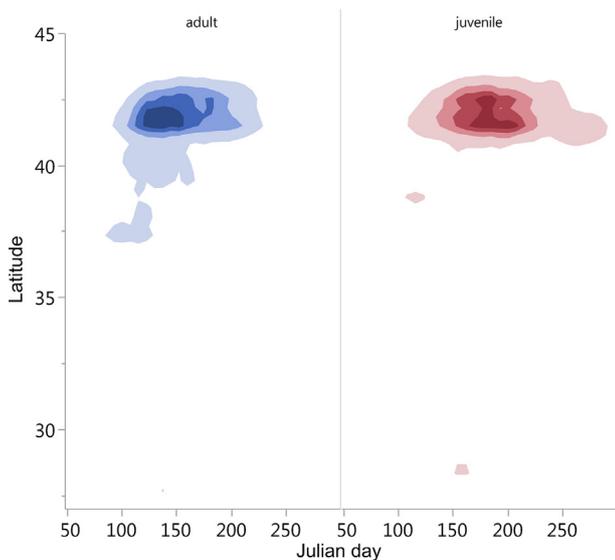


Fig. 3. Comparison of the relative number (density) of adult and juvenile quail records at various degrees of latitude and Julian date. Density increases from light to dark.

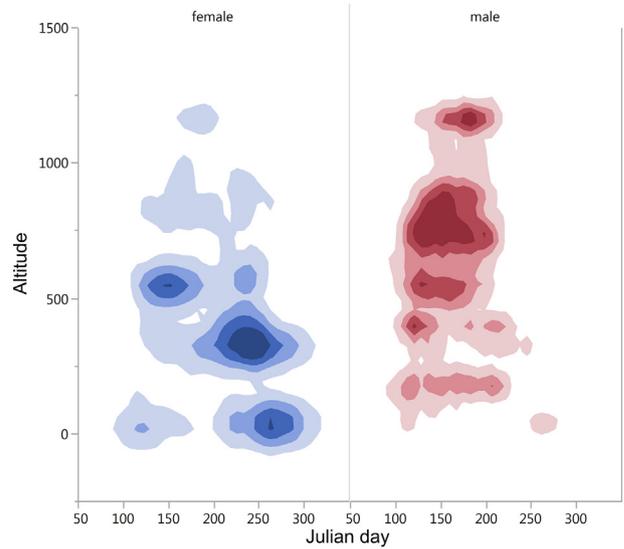


Fig. 4. Comparison of the relative number (density) of male and female quail records for meters of altitude and Julian date. Density increases from light to dark.

rainfall and temperature differed between years, and weather variables affected the resulting age and sex models. For the age models, the overriding weather variable was the rainfall at departure, followed by the temperature at arrival; in the sex models, winter temperature was the overriding weather variable, followed by rainfall during the stay, and rainfall at arrival.

4. Discussion

We aimed to assess the effects of geography and weather conditions on the probability of quails belonging to different age and sex classes to be ringed during the different stages of their annual migration cycle. By analyzing a long term ringing dataset, our results suggest that date accounts for most of the variation in the distribution of both, age classes and sex. These results propose that adults have earlier waves of arrival to the breeding sites than juveniles (Angeletti et al. 2012). In particular, our results show successive waves of adult movement, followed by waves of juveniles from the same ringing sites, and from more southern latitudes. The dominant factors in the first age models were the date of capture, followed by the rainfall at departure, and the temperature at arrival (Åkesson 2016; Boswell et al. 1993; Dossman et al. 2016). These results support the notion that waves of quail arrival in the breeding areas

Table 3

Differences on the average Julian date of capture (\pm standard error) according to the age-class in the different studied areas.

	Date adult	Date young	F	P value
Canary Islands	113.8 \pm 1.3	141.6 \pm 1.6	178.1	<0.0001
Ceuta and Melilla	118.1 \pm 9.1	136.9 \pm 1.0		
Central South	128.9 \pm 0.5	157.2 \pm 1.1	525.5	<0.0001
Balearic Islands	141.9 \pm 1.6	168.9 \pm 3.0	61.9	<0.0001
Ebro Valley	152.3 \pm 0.5	206.8 \pm 0.5	6065.2	<0.0001
Duero Valley	152.9 \pm 0.4	177.9 \pm 0.5	1384.3	<0.0001
North Plateau	161.4 \pm 0.5	168.1 \pm 0.5	108.6	<0.0001
North	160.0 \pm 0.4	184.6 \pm 0.5	1604.1	<0.0001
	Date male	Date female	F	P value
Canary Islands	124.7 \pm 30.4			
Ceuta and Melilla	131.1 \pm 11.3	133.7 \pm 13.4		
Central South	133.9 \pm 0.5	187.6 \pm 3.6	215.7	<0.0001
Balearic Islands	150.3 \pm 3.0	146.2 \pm 7.6	0.3	>0.6
Ebro Valley	167.8 \pm 0.4	223.7 \pm 1.4	1533.0	<0.0001
Duero Valley	160.2 \pm 0.3	197.1 \pm 5.2	51.1	<0.0001
North Plateau	165.3 \pm 0.3	196.2 \pm 5.1	35.8	<0.0001
North	169.2 \pm 0.3	204.8 \pm 2.6	188.2	<0.0001

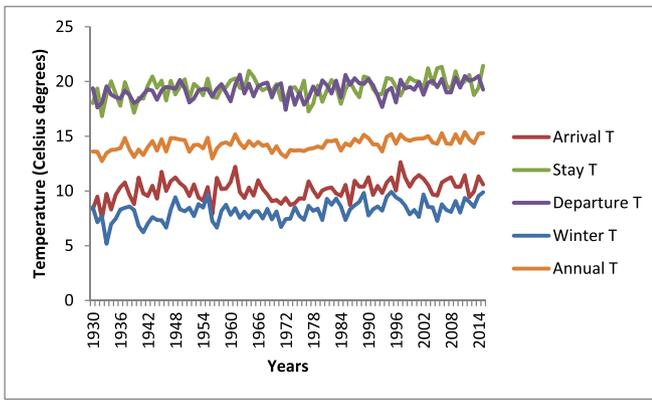


Fig. 5. Monthly average temperature in quail migration stages over time: Celsius degrees of temperature at arrival (Arrival T), temperature during the stay (Stay T), temperature at departure (Departure T), winter temperature (Winter T), and the average over all stages (Annual T).

comprise both migratory and nomadic movements. Because rainfall and temperature both vary from year to year, the timing of green waves of plant productivity, harvest dates, and peak net primary production change yearly (Deng et al. 2017; Sun and Du 2017; Yang et al. 2008). Likewise, breeding attempts depend on variations in resource abundance, which are related to weather (Mares et al. 2017; Pillar et al. 2015). Quail leave the breeding area after the harvest and adults begin to set off earlier than juveniles, so that juveniles are most numerous during the departure stage. This indicates that the migratory patterns of adults and juveniles differ (Seifert et al. 2016; Wilson et al. 2017). This is to be expected; for example at latitude 42° N, adult and juvenile quail were ringed in April and May, respectively, so that more ringed adults were encountered in May than juveniles. Conversely, more juveniles than adults were ringed in June (Sergio et al. 2014; Streby et al. 2015).

The sex models suggest that males arrive earlier at stopover and breeding sites than females. The waves of population movement by males appear to be separated from those of females (Angeletti et al. 2012; Møller 2004). These differences between males and females separate the sexes at breeding sites by latitude and altitude and relate to the dates of the green wave, herbaceous plant maturation, and small-grain cereal harvests. Quail breeding attempts follow this sequence of herbaceous plant growth, and the arrival dates of males and females at higher altitudes differ between the sexes; males arrive and depart sooner than females (Alves et al. 2013; Visser et al. 2009). This phenomenon can be partially explained by the fact that male and female

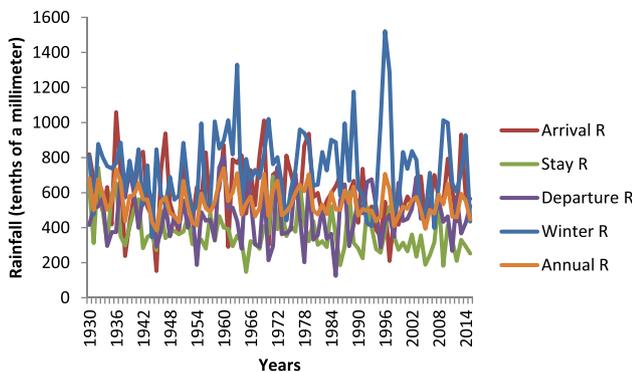


Fig. 6. Monthly average rainfall (tenths of a millimeter of precipitation) in quail migration stages over time: rainfall at arrival (Arrival R), rainfall during the stay (Stay R), rainfall at departure (Departure R), winter rainfall (Winter R), and the average over all stages (Annual R).

quail were generally ringed in April and May, respectively, so it is to be expected that more ringed males would be encountered in May than ringed females, and more ringed females in June than in May. Spatio-temporal sex segregation allows quail to disperse and aggregate, and to link localities (latitude and altitude) with breeding attempts (herbaceous ripening) (Butler and Norris 2013; Visser and Sanz 2009). This is probably a strategy to avoid predation (through dispersion) on the one hand and to facilitate successful breeding (through aggregation) on the other. In contrast, each breeding attempt requires quail to aggregate at high density to enable sexual selection and mating (Tøttrup et al. 2010; Välimäki et al. 2016; Zúñiga et al. 2016). Females drive males away after mating and do not solicit them again until the next breeding attempt (Nadal and Ponz 2015). Further research on quail convergence and divergence is clearly needed to better understand the interplay between their movements between stay areas and their spatial dispersion and aggregation.

Our results show that the most important factors in models of age and sex were the date of capture followed by latitude or altitude, and the weather variables (Eikenaar and Schläfke 2013; Erni et al. 2002; Gwinner 1996). These results suggest that in both models (age and sex) the presence of quail can be explained by the ripening date of cereal crops (time: i.e. arrival, stay and departure) and geographic area (space) (La Sorte et al. 2016; Lavee et al. 1991; Sarda et al. 2012). In fact, the waves of movement of population groups (age and sex) follow the green waves and the pull of conspecific attraction (Safriel and Lavee 1988; Verhoeven et al. 2018; Wingfield 2008). In both models, the date of capture is the dominant influencing factor, reflecting the timing of the movement and stay stages of quail. These movements are related to feeding and breeding behaviour, and the distance moved and dates of movement are dynamic, and change between years (Newton 2007; Reif and Hanzelka 2016; Williams et al. 2015). In practice, latitude reflects migratory (long distance) movements, whilst altitudinal movements suggest nomadic (short distance) movements (Kosicki et al. 2014; Morrison et al. 2013; Streby et al. 2015). Both models agree with the view that itinerant breeding behaviour is the best strategy to exploit the available resources. Quail undertake consecutive nesting attempts in two or more geographically separate regions (north Africa, and southern and central Europe) (Seifert et al. 2016). The changes in capture probability might be related to the influence of stopovers, particular geographical routes, or the timing and location of stays on site fidelity and philopatry (Hedenström 2008; Jahn et al. 2016; Norris 2005; Ockendon et al. 2012; Pedersen et al. 2016).

Our models contribute to the understanding of the complexities of the quail's strategy. Age and sex models correspond with waves of quail movement and stages because quail segregate into age and sex groups, and this is related to breeding attempts. Logistic models support the idea that movements and stages are interrelated. This new interpretation of quail life history provides a possible explanation for their success as a migrating population exploiting anthropic landscapes (villages, croplands and rangelands) (Moss et al. 2010; Pedersen and Krøgli 2017; Walther 2016). We recommend improving the detail collected in ringing databases to improve the results of studies using ringing data, thereby improving research activities across organizations and institutions. Such improvements in collaboration could lead to more effective management and conservation of migratory bird populations. Measures to conserve quail require the identification of the essential geographical areas that they use (Deluca et al. 2015; Greenwood 2003; Moreira et al. 2005) in the course of their complex life history strategy.

Quail as a migratory bird is subject to the environmental quality of Africa and Europe. The environmental conditions of both continents reflect their socio-economic situation. We have studied the conditions for quail in the Southwest of Europe which is relevant for the breeding period; however the Sahel in Africa is relevant for the wintering period. The survival of migratory birds needs environmental quality in both, breeding and wintering grounds, so it is urgent to apply conservation measures on a global view considering large scale ecological processes

and transboundary cooperation (Wiens and Bachelet 2010; Rands et al. 2010).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.08.345>.

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