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Population age structure as an indicator for assessing the quality of breeding areas of Common quail (*Coturnix coturnix*)

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ABSTRACT

Quality breeding areas are vital for the management and conservation of migratory bird species, especially those under pressure from climate warming effects. The Common quail *Coturnix coturnix* is a migratory species characterized by its itinerant breeding (several breeding attempts in different places) and exposure to high mortality rates, and it is a case in point. The identification and management of high quality nesting areas is essential to conserve this and other migratory species. Here, we use a Spanish long-term quail ringing dataset (1961–2014) to correlate population age structure with temporal and geographical variables. We show that northern Mediterranean regions provide optimal breeding sites and have balanced population age structures (young:adult males). The proportion of young:adult males provides an indicator of the relative quality of various breeding areas. Records of ringed quail provide data on the overlap between young and adult males temporarily resident in different geographic areas and may provide a useful tool to evaluate habitat quality. We found that the timing of sequential breeding attempts and temporary residency of quail are associated with latitude, altitude, and geographic location of quail ringing records. In southern regions, young males arrive at the breeding area later than adults, while in northern regions young birds and adults arrive at same time. Optimal breeding areas are characterized by high quality habitat, have high quail densities, and a mixture of young and adult males, factors that favour sexual selection, heterozygosity and population viability. However, not all high quality habitat areas are suitable for reproduction, being necessary enough quail density and the adequate proportion of young:adult males.

1. Introduction

Effective wildlife conservation requires ever increasing knowledge regarding breeding areas to improve the application of management measures to encourage reproductive success (Pe'er et al., 2014). Among the factors affecting the quality of breeding habitats and wildlife reproduction, climate change is gaining importance and is a key factor in explaining most recent instances of population decline. Changes in rainfall and temperature have an impact on plant and animal biological cycles (i.e. breaks and desynchronization) affecting their ecological functions (i.e. alter species assembly) and ecosystem services (i.e. provisioning, regulating, supporting and cultural services). Migratory bird species that select nesting areas according to habitat quality (Møller, 2004; Germain et al., 2015) are also affected, leading to impacts on their reproductive success and population viability (Stodola and Ward, 2017).

The Common quail (*Coturnix coturnix*) is an Afro-Palearctic migratory bird (Galliform, Phasianidae) that the current trend in Europe is decreasing in some countries and stabilized in others. Quail has a complex life history strategy characterized by itinerant reproduction involving several breeding attempts separated by altitudinal and latitudinal movements (Rodríguez-Teijeiro et al., 2009). In the Iberian Peninsula, for example, the first breeding residency, termed 'stay' in this paper, (early attempt) takes place in southern areas, the second (middle attempt) occurs in the central Iberian Peninsula, and the third (late attempt) occurs in the north (Nadal et al., 2018). Because of its continuous nomadic and migratory movements, the species is exposed to high mortality rates, balancing its survival/mortality chances to avoid jeopardizing population viability (Rushing et al., 2016; Kempenaers and Valcu, 2017).

The cycle of plant ripening is influenced by geography and meteorology, and it forces quail to change nesting grounds as the year progresses (Kaiser et al., 2015) to shynchronize breeding stays with plant maturation and harvest (Seifert et al., 2016). The quality of any breeding area is ephemeral due to changes in plant condition, and the abundance and dispersion of conspecifics (Gunnarsson et al., 2005). As

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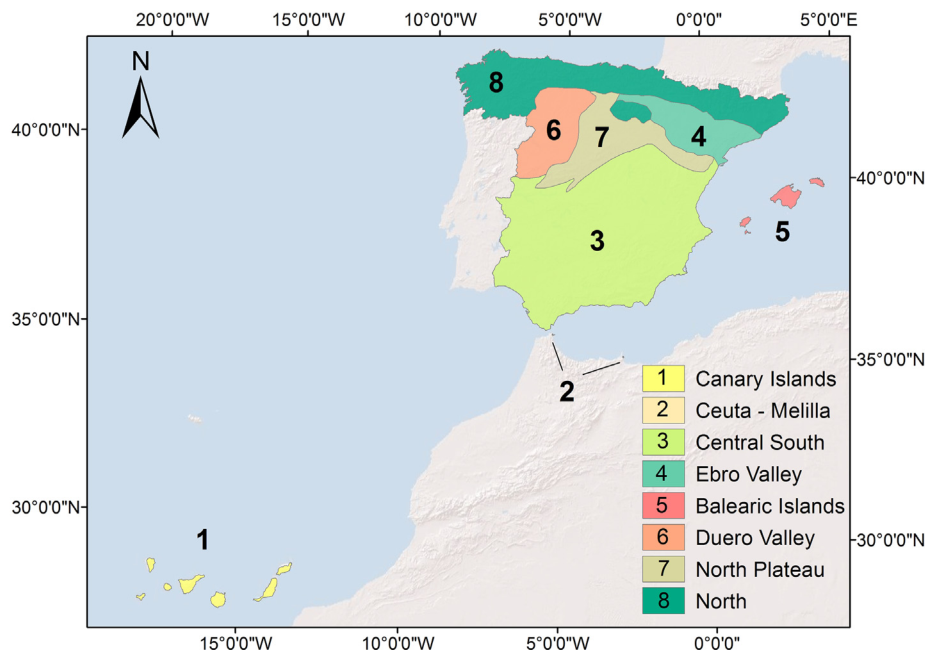

Fig. 1. Geographic distribution of cloudy areas according to the images of Wilson and Jetz (2016).

Table 1
Quail habitat quality indices for the geographic areas studied.

Geographical area	Habitat (ha)	Harvest period	Habitat suitability index	Percentage of irrigated land	Productivity index
Canary Islands	131,002	April–May	0.4–1	0	5.46
Ceuta Melilla	0	April–May	0–0.4	0	–
Central South	10,328,435	May	0.4–1	5.61	3.96
Ebro Valley	2,001,987	June–November	1–0.4	19.11	3.69
Balearic Islands	78,363	June	0.4–1	6.11	4.84
Duero Valley	2,552,431	July–November	1–0.4	11.26	6.09
North Plateau	2,230,423	July–August	0.7–1	7.11	6.68
North	1,391,677	July	0.1–1	2.27	4.36

Table 2
Fitted curves for young and adult males for critical Julian date of ringing and rate of population growth, according to geographic area.

	Adult		Young	
	Critical date	Rate of growth	Critical date	Rate of growth
Canary Islands	112.37 ± 2.27	27.04 ± 2.35	147.30 ± 4.55	31.77 ± 4.56
Ceuta Melilla	120.78 ± 3.79	20.14 ± 3.80	149.60 ± 10.93	38.46 ± 11.05
Central South	136.61 ± 0.51	20.48 ± 0.51	154.26 ± 4.92	34.93 ± 4.94
Ebro Valley	138.32 ± 0.93	27.27 ± 0.93	204.04 ± 2.07	41.06 ± 2.09
Balearic Islands	142.89 ± 1.44	20.62 ± 1.44	172.16 ± 11.31	36.63 ± 11.32
Duero Valley	147.18 ± 0.71	27.34 ± 0.71	182.53 ± 1.69	27.43 ± 1.69
North Plateau	159.73 ± 0.96	25.06 ± 0.96	167.08 ± 0.93	24.52 ± 0.93
North	159.46 ± 0.87	28.68 ± 0.87	183.04 ± 1.02	19.56 ± 1.02

the breeding season progresses, birds move to higher latitudes or altitudes in the same or different geographic areas (Ruiz-Gutierrez et al., 2016) to follow the optimal habitats for each nesting attempt (Wiegardt et al., 2017). As a result, the geographical distribution of 'cloudy areas' (in the sense of Wilson and Jetz's 2016 study of cloud distribution) fits the sequence of breeding residencies of this species (Ockendon et al., 2013).

The quail's life history involves rapid development (1 month), with the achievement of sexual maturity at an early age (2 months), and a low average life expectancy (9 months) (Estrada et al., 2016). During the reproductive period, males gather at breeding areas in greater numbers than females (Angeletti et al., 2012) and young (younger than 6 months) and adult (older than 6 months) males compete for mates (Nadal and Ponz, 2015). Although young and adult males aggregate on the breeding grounds (Samplonius and Both, 2017), the young:adult male ratio during the reproductive period is generally unknown. A breeding attempt requires about 50 days and females only accept males during the pre-laying and laying period (Thys et al., 2017). Therefore, in optimal breeding areas we should expect higher quail densities and greater rivalry (i.e., a balanced proportion of young vs adult males), while in suboptimal areas we should expect lower densities and a lack of competition.

Here we aim to explore the differences in the male age-structure in both optimal and suboptimal nesting habitats. We used Spanish long-term quail ringing datasets (1961–2014) to correlate male age distribution with temporal and geographical variables. For each defined

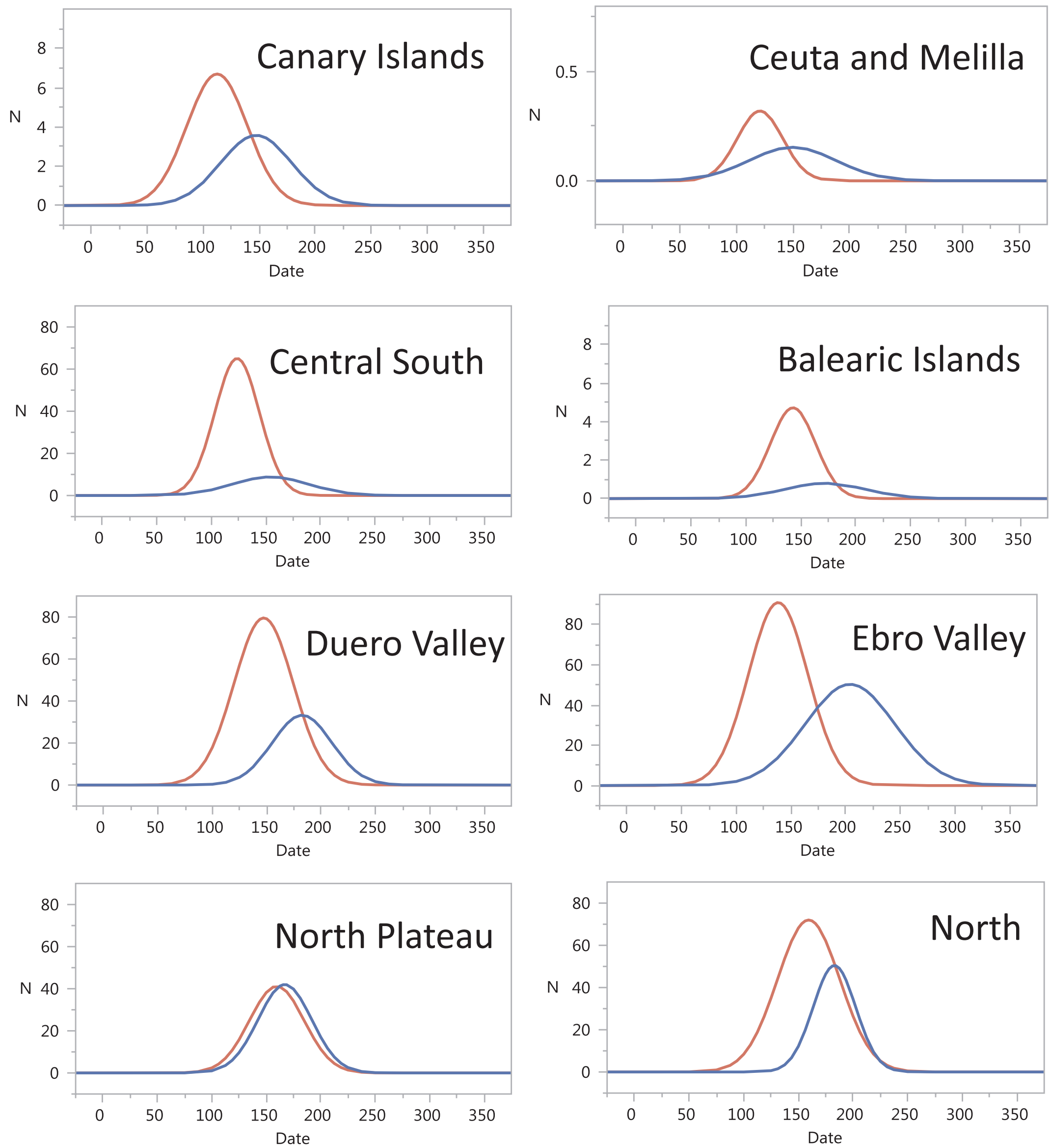

Fig. 2. Number of adults (red) and young (blue) banded male quails according to Julian date. Note the different Y axis for the Canary Islands, Ceuta-Melilla, and the Balearic Islands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
P-values of the equivalence tests for overlap in ringing date curves for young and adult male quail, according to geographic area. The curves for young and adult males are separated when the maximum values, critical points, and rates of population growth show significant differences. NS: non-significant.

	Adult-young fit curves comparison		
	Maximum value	Critical point	Rate of growth
Canary Islands	< 0.05	< 0.05	< 0.05
Ceuta Melilla	< 0.05	< 0.05	< 0.05
Central South	< 0.05	< 0.05	< 0.05
Ebro Valley	< 0.05	< 0.05	< 0.05
Balearic Islands	< 0.05	< 0.05	< 0.05
Duero Valley	< 0.05	< 0.05	NS
North Plateau	NS	NS	NS
North	< 0.05	NS	< 0.05

breeding area we calculated the temporal distribution curves for young and adult males. We then compared the curves using the maximum abundance, the critical point (date when the slope of the curve changes), and the population growth rate. The critical date, when the trend in ringed quail numbers changes, represents the point at which fewer birds arrive in an area than leave it.

Our main objective was to analyze the presence of young and adult males according to date, from the Canary Islands to the northern Iberian Peninsula. We hypothesized that both young and adult males would be present in optimal breeding areas, while age-class asymmetries would be seen in suboptimal breeding areas (Doligez, 2002). In this way we tried to discriminate between optimal and suboptimal nesting regions, using age-date models that correlate geographic areas with population structure and productivity (Szczys et al., 2017). To interpret the results we used several ecological indicators of habitat quality for the studied geographical areas.

2. Methods

2.1. Data collection

We obtained 43,194 historical quail banding records from a number of Spanish ringing organizations, all relating to the period from 1961 to

Table 4
AICc (corrected Akaike information criterion), BIC (Bayesian information criterion) and R^2 (coefficient of determination) for assessing the Gaussian models of young and adult males in different geographic areas.

Geographical area	N	AICc	BIC	R^2
Canary Islands	720	2706	2734	0.32
Ceuta Melilla	33	64	94	0.09
Central South	4382	3751	3781	0.83
Ebro Valley	11,952	4635	4665	0.72
Balearic Islands	319	1969	1999	0.38
Duero Valley	7731	4172	4202	0.82
North Plateau	5034	3830	3860	0.78
North	7619	4265	4295	0.79

Table 5
Multiple regression models of Julian date of ringing in different geographic areas for young and adult males by altitude and latitude (n = 8). Significant results are shown in bold.

	Adults	Young
R^2	0.93	0.53
Model (F statistic)	31.35	2.90
Model (P error)	**0.0015**	0.15
Altitude effect (F statistic)	7.33	0.13
Altitude effect (P error)	**0.042**	0.73
Latitude effect (F statistic)	33.81	5.46
Latitude effect (P error)	**0.0021**	0.07

2014. This included 37,706 records from SEO/BirdLife (ICONA rings), 4209 records from hunters' associations (FEDENCA rings) and regional governments (Junta de Castilla y León, Cabildo de Tenerife rings), and 1279 records from the Sociedad de Ciencias Aranzadi (ARANZADI rings). We filtered and homogenized these three datasets to contain information on the same variables: Julian date, latitude and altitude. We then had 37,790 records for this study. The quail in this dataset were captured on the breeding grounds for ringing mainly using horizontal nets and female lures during the day. The temporal and spatial distributions of the ringing teams were associated with the presence and abundance of quail in the locality. Because ringing effort is proportional to reward of quail ringed, the quail presence and effort applied to ring are related. Accordingly, the number of ringed quail is proportional to their abundance. We mapped eight cloudy areas from the Canary Islands to the northern Iberian Peninsula according to the images of Wilson and Jetz (2016) (Fig. 1). We associated each quail ringing record with a single geographic (cloudy) area.

2.2. Ecological indicators of habitat quality

We assessed the nesting habitat quality of each cloudy area to provide a quality index using: a) the amount of habitat suitable for quail (hectares of herbaceous crops and grassland) (Kosicki et al., 2014); b) the harvest period (Rushing et al., 2016); c) the habitat suitability index during the harvest period (Sarda et al., 2012); d) the percentage of irrigated land in the suitable area (Butler and Norris, 2013); and e) the quail productivity index (Cadahía et al., 2017) (Table 1). In addition, we needed to bear in mind that many breeding attempts fail due to unfavorable agricultural practices (run over, eliminate cover, pesticide applications and habitat destruction) and predator activity (Laidlaw et al., 2017; Martínez-Abraín and Jiménez, 2016). Land covered by cereals, alfalfa, corn, sorghum, sunflower, cotton, grasslands and meadows were considered to provide good quail habitat. The crop harvest period is critical in determining optimal habitat availability, because after harvest farmers plow the land and the quail habitat disappears. Habitat suitability indices varied from 0 to 1 (we set the range for each geographic area) based on normalized difference vegetation index (NDVI) satellite images taken during the breeding period, just previous to harvest when cereal and herbaceous crops has more cover. On irrigated land the range drops owing to the succession of different crops, and the resulting longer period of crop ripening leads to an extended period with enough plant cover to provide suitable quail habitat. We produced an index of quail productivity using the average young:adult quail ratio from hunter's bag records at the end of summer and beginning of autumn.

Conditions on the Canary Islands, are peculiar in several ways: a) quail are especially aggregated because the amount of useful land available is about one thousandth of that found in the other geographic areas (indeed each archipelago includes several islands without any continuous habitat availability); b) the impact of predation is much lower than on the continent due to the smaller number of predator species and their lower density; and c) the weather on the islands is more favourable for reproduction. These factors all play a role in making islands better breeding habitats than continental areas, and this is indicated by their high quail productivity index (Schluter and Repasky, 1991).

2.3. Statistical analyses

We used non-linear fitted curve models to assess the numerical distribution of male quail according to age (young:adult) by ringing date for each geographic area. We created the curves using the Gaussian Peak model, which is a scaled version of the Gaussian probability density function (SAS, 2015). The equation for the predictive model includes: a = the point of maximum number of quail; b = the critical point (inflection date); and c = the rate of population growth.

$$a{*}\mathrm{Exp}\left[-\left[0.5{*}\left[\frac{(\mathrm{Date}-b)}{c}\right]^2\right]\right]$$

We compared these parameters between curves for young and adult males in each geographic area. The AICc (corrected Akaike information criterion), BIC (Bayesian information criterion) and R^2 (coefficient of determination) were calculated to confirm the relative statistical quality of the curves for young and adult males (Burnham and Anderson, 2002). We used Graph Builder in JMP12 (SAS, 2015) to represent the distributions of young and adult ringed males, according to latitude and altitude, and for all geographic areas. Multiple regressions were performed to explain the average ringing date of young and adult males by latitude and altitude, and to determine if for both age classes the average of ringing date is explained in the same way.

3. Results

The date at which the trend in the number of ringed quail changed (critical date for the young and adult curves) increased progressively with increase in latitude from the Canary Islands to the northern Iberian Peninsula. For adult males, the Balearic Islands were an exception; their critical date was later than would be predicted by their latitude (cf. the critical date for the Ebro Valley). On the contrary, the Balearics were not an exception for young males; the critical date advanced in the sequence Canary Islands, Ceuta Melilla, Central South, North Plateau, Balearic Islands, Duero Valley, North and Ebro Valley (see the order of critical dates, Table 2, Fig. 2).

Testing the equivalence between young and adult male curves for the maximum numbers of ringed quail, critical date and rate of population growth, only the North Plateau showed no significant differences in any of these parameters. In this area, both young and adult males showed entirely overlapping curves. In all of the other geographic regions, the young and adult curves were significantly different (Table 3 and Fig. 2).

The determination coefficients of the models were similar for the various Peninsular areas, about half this value for the Island areas, and not significant for Ceuta-Melilla. However, the AICc and BIC were

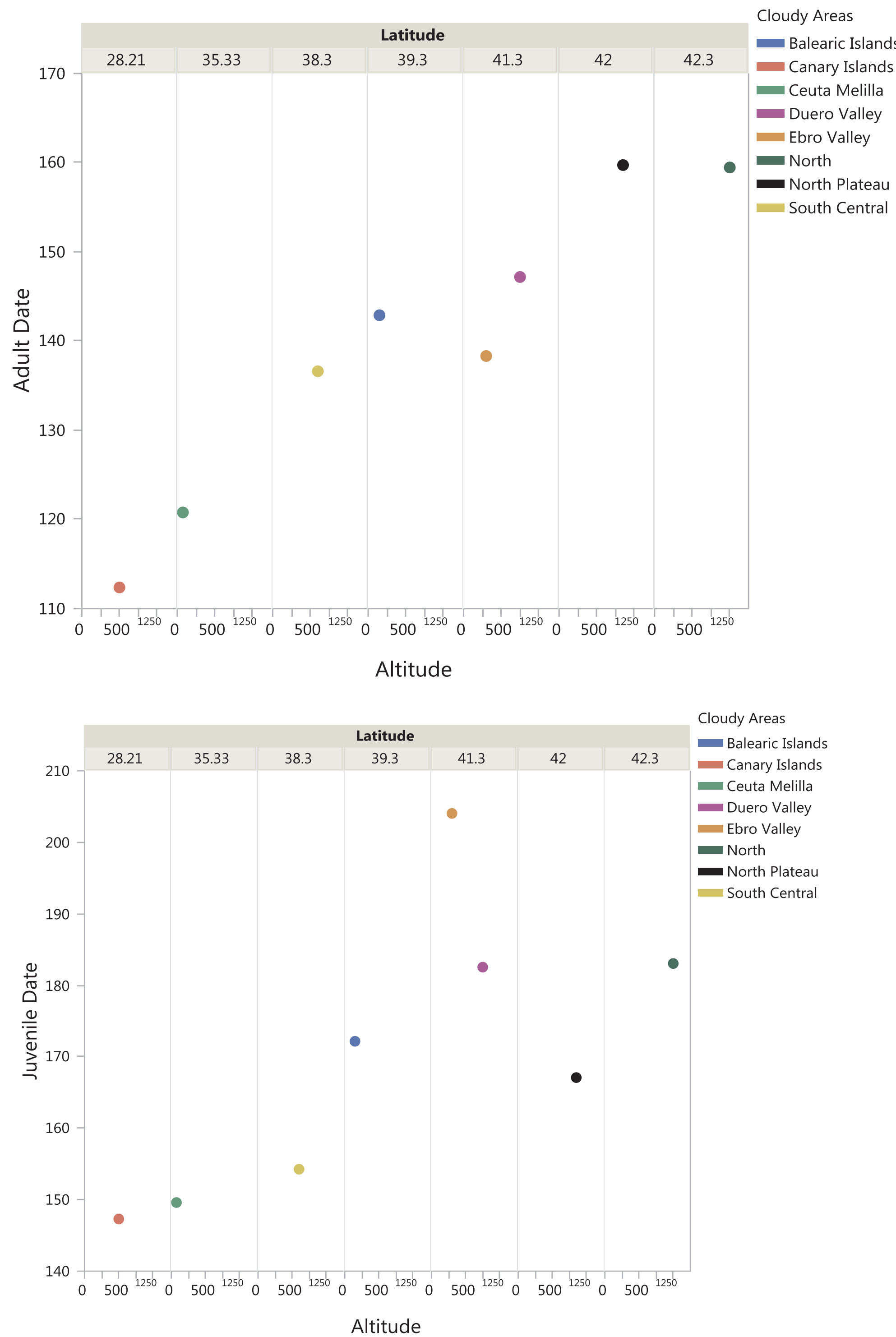

Fig. 3. Graphs of Julian critical date and ringing date of young and adult males, according to latitude, altitude and geographic area.

similar for all areas except Ceuta-Melilla, probably due to the small dataset for this region. In practice, only areas with more than one thousand records provided sufficient information to compare the models between both age classes (Table 4 and Fig. 2). Multiple regression models for ringing date by altitude and latitude were significant for adult males, but not for young males (Table 5). Over time, both young and adult males move to higher latitudes and altitudes, and to higher quality areas (Table 2 and Fig. 3). However these movements are clearly ordered in adults and erratic in young.

4. Discussion

Our findings suggest that the critical date of the number of quail ringed may provide a useful tool to assess the overlap between young and adult male stays in different geographic areas (Alves et al., 2013a,b; Mayor et al., 2017). The quality of a breeding area depends not only on plant cover, the agricultural cycle and predation pressure, but also on conspecific abundance (Marra et al., 2015; Lehikoinen et al., 2017). When the stays of young and adult males in a breeding area overlap, the number of individuals is higher, thus increasing competition and the availability of males for mate selection (Piper et al., 2013; Bijleveld et al., 2016). Optimal breeding areas, such as the North Plateau, showed high quail density and the presence of both young and adult males, while in suboptimal breeding areas (i.e., the other geographic areas, Fig. 2) the overlap was incomplete. It is important to note that the simultaneous timing of stays of young and adult males is not possible in all geographic areas for two reasons. First, the quail's migratory and nomadic lifestyle results in sequential breeding stays in different areas (Freckleton et al., 2006; Lupi et al., 2017). Adult males abandon a breeding area sooner, moving to higher altitudes and latitudes (Table 2), followed by young males later on (Alves et al., 2013a,b; Cirule et al., 2017). We can therefore assume that low latitude breeding areas are not optimal for breeding, because they always attract fewer young males than adults, and because the young ones arrive later on in the year (Grist et al., 2017). Secondly, plants ripen earlier in southern than in northern areas. This would explain why young and adult males do not coincide in southern areas, as these regions would have fewer young males than most northern areas (Suárez-Seoane et al., 2017). Conversely, in optimal areas (i.e., the North Plateau) young and adult males coincide and the number of individuals in each class is similar.

The quality of a nesting area depends on the amount of useful habitat and the percentage of irrigated land, which can extend the time during which habitat conditions are optimal (Taylor, 2017). For example, the greatest amount of suitable habitat occurred in the Central South, which is also the most extensive zone (Table 1). The climate of a geographic area determines the harvest period (which may be prolonged by irrigation) and affects the period of stay of the quail, as in islands and valleys (Vernasco et al., 2018). The habitat suitability index combines the period of time stayed with the distribution of good quality habitat (Godet et al., 2018). Accordingly, the North Plateau is an advantageous zone with high quality habitat conditions. The quail productivity index may be an indicator of high quality nesting areas because optimal habitats lead to higher productivity (McKinnon et al., 2010; Pedersen and Krøgli, 2017). Our results support this hypothesis because areas such as the North Plateau, the Duero Valley and the northern Peninsula showed higher productivity values. Following this logic, islands (Balearic and Canary Islands) are an exception because of their high quail densities, low predation rates and mild climates (Morrison et al., 2013).

Young and adult males show different characteristics in all of the geographic areas studied (Fig. 3); the number of adults fits well with the time advance model whereby numbers progressively increase with latitude and altitude (Table 5). However, the number of young do not follow this model so well, because their numbers depend on previous breeding successes in southern areas (Raja-aho et al., 2017). Consequently, the arrival date of young males in a nesting area is a characteristic of each geographic zone (Åkesson et al., 2017). The presence of irrigated land with alfalfa, maize, fodder, and sorghum lengthens the time during which an area offers suitable habitat for reproduction (Perez et al., 2017). The Duero and Ebro Valleys have irrigated land which provides more suitable habitat than is found in the drier land surrounding them. However, quail productivity is substantially different between these two valleys, possibly as a result of altitude and climate differences, Duero being higher and cooler. The North Plateau is similar to other central European areas, being cooler and wetter than Mediterranean regions. However, young males arrive in northern Spain and other European breeding areas over a shorter period, and therefore fewer young males attempt to reproduce there (Woodworth et al., 2017).

Our results show that optimal breeding areas have good quality habitats and harbor higher densities of male quail, both young and adult (Willemoes et al., 2017). In contrast, suboptimal breeding areas do not show so much overlap between young and adult male visits, and have lower habitat quality indices (Fern and Morrison, 2017). Sexual selection requires the spatial and temporal overlap of young and adult males, and competition and rivalry is fostered by the greater availability of opportunities for females to choose mates (Mariette et al., 2015). The North Plateau area has the best resources for quail breeding; optimal quality habitat and the best population structure (Taylor and Stutchbury, 2016). The best population structure and habitat resources encourage the most productive reproductive effort. Consequently, from a conservation perspective (Bairlein, 2016), optimal breeding areas such as the North Plateau, should be a priority for management and conservation measures, because they have the most potential to guarantee population viability.

5. Additional information

We have no competing interests

6. Data accessibility

Banding data for this study were provide by SEO: https://www.seo.org, ICO: http://www.ornitologia.org/ca/, ARANZADI: http://www.aranzadi.eus/category/ornitologia, FEDENCA: https://www.fecaza.com/fedenca.html, FCCL: http://fedecazacyl.es, Cabildo de Tenerife: http://www.tenerife.es/portalcabtfe/es/.

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