Breeding in a Dry Wetland. Demographic Response to Drought in the Common Reed-Warbler Acrocephalus scirpaceus

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BREEDING IN A DRY WETLAND. DEMOGRAPHIC RESPONSE TO DROUGHT IN THE COMMON REED-WARBLER *ACROCEPHALUS SCIRPACEUS*

REPRODUCCIÓN EN UN HUMEDAL SIN AGUA. RESPUESTA DEMOGRÁFICA DEL CARRICERO COMÚN *ACROCEPHALUS SCIRPACEUS* A LA SEQUÍA

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Summary.—Mediterranean wetlands show remarkable seasonal and annual variations in their hydroperiod, i.e. the period during which they are inundated. Climate change-induced hydroperiod reductions have been shown to affect marshland birds but more studies are needed to understand this process in Mediterranean wetlands. The present study shows the demographic response of the Common Reed-warbler *Acrocephalus scirpaceus* to an unusual and prolonged drought in the Tablas de Daimiel National Park wetland (central Spain). We used data from two constant effort mistnetting stations (2005-2013), and spatially explicit capture-recapture Jolly-Seber models. The Reed-warblers continued reproducing in a dry environment for three years after the start of a dry phase, despite progressive declines in productivity, and ultimately stopped nesting in the fourth year. After the recovery of water levels in subsequent years, the population required another four years to recover a size and productivity similar to those preceding the drought. This situation may be common in the near future given ongoing alterations of the hydroperiod in Mediterranean wetlands as a consequence of climate change and groundwater overexploitation. We also show that spatially explicit capture-recapture models allow the detection of changes in the populations of small passerines, and are an accurate approach to estimating their densities. —Jiménez, J., Hernández, J.M., Feliú, J., Carrasco, M. & Moreno-Opo, R. (2018). Breeding in a dry wetland. Demographic response to drought in the Common Reed-warbler *Acrocephalus scirpaceus*. *Ardeola,* 65: 247-259.

Key words: bayesian, bird density, fluctuation, hydroperiod, monitoring, productivity, Spatial Jolly-Seber, wetland.

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RESUMEN.—Los humedales mediterráneos muestran notables variaciones estacionales y anuales en su hidroperíodo, o período de tiempo durante el cual el humedal está inundado. Se ha demostrado que las reducciones del hidroperíodo inducidas por el cambio climático afectan a las aves palustres, pero se precisan más estudios para comprender este proceso en los humedales Mediterráneos. El presente estudio muestra la respuesta demográfica del carricero común *Acrocephalus scirpaceus* a una inusual y prolongada sequía en el Parque Nacional de Las Tablas de Daimiel, humedal situado en el centro de España. Utilizamos los datos de 2005 a 2013 de las estaciones de anillamiento de esfuerzo constante del parque, y modelos Jolly-Seber espacialmente explícitos de captura-recaptura. Observamos que la especie siguió reproduciéndose en un ambiente seco durante tres años después del inicio de una fase seca –aunque con una progresiva disminución de la productividad– y finalmente dejó de reproducirse en el cuarto año. Después de la recuperación de los niveles de agua, la especie requirió otros cuatro años para recuperar un tamaño de población y productividad similares a los anteriores a la sequía. Esta situación puede ser común en un futuro próximo según las previsibles alteraciones del hidroperíodo en los humedales mediterráneos como consecuencia del cambio climático o el aumento de la sobreexplotación del agua subterránea, lo que afectaría la dinámica poblacional del carricero común y otras especies de aves palustres. También mostramos que los modelos de captura-recaptura espacialmente explícitos permiten la detección de cambios en las poblaciones de pequeños paseriformes y son un enfoque preciso para estimar sus densidades. —Jiménez, J., Hernández, J.M., Feliú, J., Carrasco, M. & Moreno-Opo, R. (2018). Reproducción en un humedal sin agua. Respuesta demográfica del carricero común *Acrocephalus scirpaceus* a la sequía. *Ardeola,* 65: 247-259.

Palabras clave: bayesiano, densidad de aves, fluctuación, hidroperiodo, humedal, modelo Spatial Jolly-Seber, productividad, seguimiento.

INTRODUCTION

Climate change and overexploitation of water resources can severely affect the conservation and ecosystem services of wetlands (Schröter *et al*., 2005). These may significantly impact on their biodiversity, as reflected by the loss of wetland birds (Kingsford *et al*., 2016). Natural fluctuations in water levels between seasons or years are an additional complexity in Mediterranean wetlands, which can mask the response of passerine bird populations to these global changes. Recent environmental changes in the Tablas de Daimiel National Park (TDNP) are used as a case study to investigate i) the effects of those environmental factors on a common passerine bird, the Common Reed-warbler, and ii) to describe how they influence its demographic parameters.

In 2005-2010, during a prolonged drought in the Tablas de Daimiel National Park (TDNP), Common Reed-warblers nested even in the absence of water (Supplementary material appendix 2), suggesting that the population did not depend on the hydroperiod. To understand the species' dynamics in the TDNP, we implemented a spatially explicit methodology to study temporal changes in population density using data from constant-effort mistnet stations.

It is well known that demographic characteristics of migratory passerines are affected by changes in the environmental conditions of breeding and wintering areas (Newton, 2008). In the case of marshland species, the drying of the wetlands they inhabit implies a radical alteration in their habitat and makes them extremely vulnerable (Royan *et al*., 2014). Poulin *et al*. (2002) found a positive correlation between the abundance of breeding reedbed-nesting passerines and food (arthropod) availability, and showed that food availability was in turn negatively correlated to the duration of the dry phase in a Mediterranean wetland (southern France).

The spring diet of the Common Reed-warbler is based on insects wintering in reed stems, insects developing in aquatic and moist habitats, and other spring insects from outside the wetland (Frampton *et al*., 2000; Chernetsov & Manukyan, 1999; Bibby & Thomas, 1985). Drying is therefore expected to cause a change in food availability for this species and thus to affect its demography.

An optimal assessment of the demographic response of species to environmental changes should use standardised and comparable measures, such as population size or absolute density. With marked individuals, classical capture-recapture (CR) models are widely used to estimate the size of "closed" animal populations that do not change during the study period (Williams *et al*., 2002). However, CR presents two main shortcomings: the uncertainty in defining the effective sampling area (Karanth & Nichols, 1998; Efford, 2004) and an intrinsic spatially-induced heterogeneity in encounter probabilities due to the positioning of traps relative to the activity centres of individuals (Royle *et al*., 2018). Constant-effort mistnetting schemes to monitor birds have been used for a long time to evaluate temporal trends using open capture-recapture models, such as Jolly-Seber (Desante *et al*., 1995), parametrised by the POPAN model (Arnasonp & Schwarz, 1999) or the Robust design approach (Pollock, 1982), that allows estimation of abundance, recruitment and apparent survival. Nevertheless, the main problems of open non-spatial models in density estimates remain the same as in closed CR (but see Pledger & Efford, 1998). Non-spatially explicit open models provide estimates of the superpopulation size (i.e. of all the individuals with a $p > 0$ of being caught) that depends heavily on parameters that are difficult to control, such as the study area perimeter and individual home ranges. Therefore, superpopulation size estimates are very difficult to compare. Spatial capture-recapture (SCR) provides a spatial context for estimating abundance –as a sum of activity centres in a sampled area– and space use, and improves inferences of population density (Efford, 2004; Royle & Young, 2008) allowing comparison among different estimates.

Capture-based surveys in mistnet and SCR models have recently been used to monitor birds both in closed and open populations (Efford *et al*., 2004; Efford, 2004; Schaub & Royle, 2014). We used long-term data (from 2005 to 2013) of the constant-effort mistnetting stations in TDNP (La Quebrada and El Morenillo), to study the response of the Common Reed-warbler population to environmental changes. We provide implementations of a SCR Jolly-Seber model (Royle & Sutherland, 2014) in the freely available R (R Core Team, 2017) and Nimble software (De Valpine *et al*., 2017; De Valpine *et al*., 2016) that allow us to estimate temporal variation in population density and demographic parameters.

METHODS

Study area and species

The Tablas de Daimiel National Park (TDNP) (39º7'59.59''N 3º42'56.18''W) is in central Spain (Figure 1), at the confluence of the rivers Guadiana (permanent with fresh water) and Gigüela (seasonal with more saline water). Until the middle of the 20th century, this was a permanent wetland, with moderate seasonal variations. The wet season (maximum flooded area) occurs during the winter-spring period whereas the dry season (minimum flooded area) takes place during the summer-autumn period. Overexploitation of the Western Mancha aquifer for irrigation caused the loss of the Guadiana River supply beginning in the early 1980s. This produced a marked increment in water level variability and a progressive loss of water discharged into the TDNP, and a change in its flooding dynamics, with the Gigüela River becoming

the only source of water (Cirujano *et al.*, 1996) in the late 1980s. From 2005 to 2010, the drying of the TDNP was complete. Since 2010, measures to control the extraction of water from the aquifer, and exceptional rainfall, resulted in the recovery of the Guadiana River, returning the TDNP to a water regime of permanence with reduced variability. As a result, the ecosystem has undergone an evolution from a permanent hydroperiod with fluctuations (up to 1980) to a seasonal one (1980-2004), and then remained completely dry for five years (2005-2010), until returning to a situation of permanence (2010-2014).

The Common Reed-warbler is a polytypic species breeding from Europe to central Asia

Fig. 1.—Study area in Tablas de Daimiel National Park in central Spain, and locations of the constant-effort mistnet stations in El Morenillo and La Quebrada. Shaded parts show islands and higher ground.
[*Área de estudio en el Parque Nacional de las Tablas de Daimiel (centro de España) y localizaciones de las estaciones de anillamiento de esfuerzo constante de El Morenillo y la Quebrada. En sombreado, áreas emergidas/islas.*]

and North Africa. Nominate *scirpaceus* breeds in the western part of the range, from North Africa and Spain to Greece, north to Scandinavia and east to Western Russia, Ukraine and Crimea (Kennerley & Pearson, 2010). The Common Reed-warbler usually nests in reeds *Phragmites australis* (Catchpole, 1972), but breeding is also possible in drier habitats (Catchpole, 1974; Kennerley & Pearson, 2010). *Phragmites* reedbeds can be found on the shores of permanent wetlands, even occupying all the wetland area in the seasonal wetlands, since a large fluctuation of water levels determines its presence (Álvarez-Cobelas *et al.*, 2001). Currently, after the described changes in water regime, the reed is the most abundant helophyte in the TDNP (Cirujano *et al.*, 2017). Around the constant-effort mistnetting stations, the reeds were uniformly distributed and interspersed with small areas of open water.
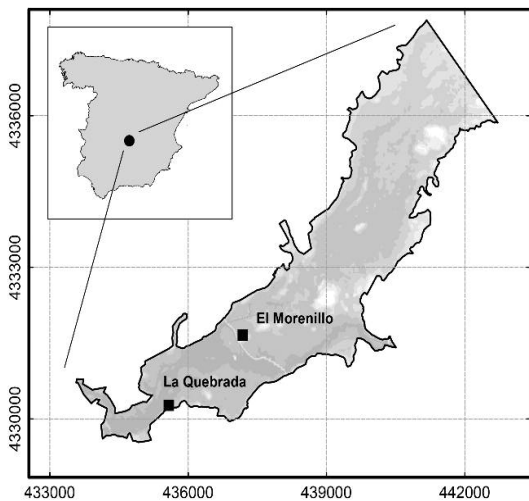
Population data and analyses

To study the population fluctuations we used ringing data from the breeding period (May 1st to July 30th) from 2005 to 2013. We discarded dates before and after this period due to the presence of migrant Reed-warblers. Hence only adult birds (Euring codes 4 or 5, Bairlein, 1995) exhibiting breeding traits (with cloacal protuberance in males and incubation patch in females) and fledglings (Euring age 3) were studied. The mistnets were set before dawn and operated for five hours after sunrise. In each session six nets (72 m) were active at the same location (Figure 2). Captured birds were ringed, weighed, aged and sexed according to Svensson (1992). We assume birds do not lose their rings. We recorded detection histories of marked birds. To prepare the data we used the secr 2.10.4 package (Efford, 2016) in R (R Core Team, 2017) as in Royle & Sutherland (2014). We assumed the population was closed within each sampling period, but could vary between years.
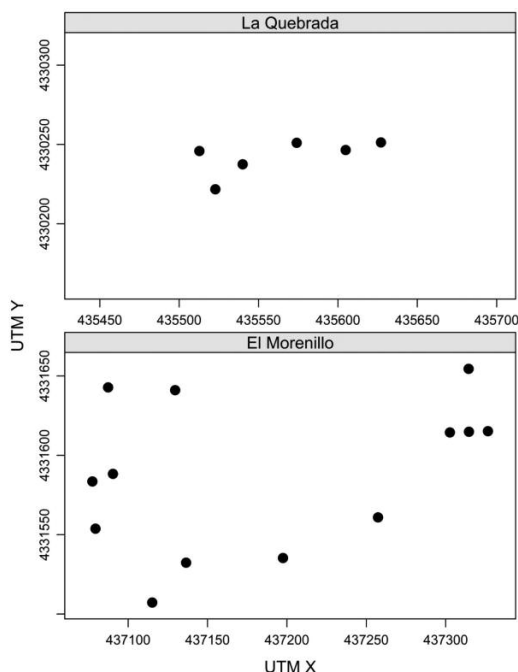
F<small>IG</small>. 2.—Locations map of the nets from the constant-effort mistnet stations in El Morenillo (below) and La Quebrada (above) at the same scale. *[Mapa de localizaciones de las redes en las estaciones de esfuerzo constante de El Morenillo (arriba) y La Quebrada (debajo), a la misma escala.]*

We used a spatially explicit Jolly-Seber model (SCR-JS) from Royle & Sutherland (2014). Spatially explicit models are extensions of classical CR that use the spatial information from traps to make inferences about the locations of the activity centres of individuals. These models postulate that an individual's encounter probability (λ_{ij}) is a decreasing function of the distance (d_{ij}) between the activity centre of individual i and the location of a survey device j (e.g., mist net) at the occasion k (Royle *et al*., 2014).

$$\lambda_{ij} = \lambda_{o} \exp\left(-\frac{d_{ij}^2}{2\sigma^2}\right)$$

Recaptures of individuals across the grid of traps are usually spatially clustered. The degree of dispersion is estimated with a parameter sigma (σ) –formally the scale parameter of half normal distribution–, which describes how detection probability declines as a function of distance from the activity centre. Another element from spatial models is the basal probability rate, or the probability of encountering an individual at its activity centre (λ_0).

SCR models can use different observation types. In our study, mistnet devices produced "multi-catch" (Efford *et al*., 2009), independent multinomial observations that can capture and hold an arbitrary number of individuals (Borchers & Efford, 2008). A statistically equivalent distribution to the multinomial is the categorical distribution, and we adopted a multinomial model in a Bayesian framework (Royle *et al*., 2014).

The SCR-JS modelling framework allows the use of SCR to deal with open populations (Supplementary material appendix 1 & 2). This spatially explicit approach can be used when the population is marked or recognisable and can be identified upon recapture. We obtained 3D histories of individual spatially-explicit encounters [i(individual), j(trap), k(occasion)] for each year. Every individual i therefore had its own activity centre s_i and all activity centres were distributed across the state space (S), defined as the area that includes the resighting grid and is sufficiently large to include all individuals potentially exposed to the survey. The position of the mistnet j (Figure 2) is the coordinate x_j, and the encounter histories included the information for each recognisable individual i trapped by mistnet j on the occasion k is y_{ijk}. We fitted the models in a Bayesian approach (see Supplementary material appendix 1 & 2).

These models produce apparent survival, recruitment, population growth rates and density (Royle *et al*., 2014). This approach has been used in birds (Schaub & Royle, 2014),

mammals (Whittington & Sawaya, 2015; Gardner *et al.*, 2010; Reppucci *et al.*, 2011), reptiles (Muñoz *et al.*, 2016) and fish (Raabe *et al.*, 2014). Ergon & Gardner (2013) and Schaub & Royle (2014) pointed out the main limitation of open methods: they can only estimate the joint probability of surviving and not emigrating from the study area between primary sessions. These authors developed similar methods that overcame this limitation, modelling the individual movement of activity centres over time as a dispersal process. Although in our study recruitment incorporates reproduction and immigration, this problem was minimised by ringing fledgling individuals only before migratory movements began. As we focused on the trend in densities (total population, adults and recruitment) across the study years, the estimate of real survival was not a limitation in our study.

We used a maximum of 14 and a minimum of six sampling sessions per year (number of weekends from May 1st to July 31st). For the resulting data set, the within-session recaptures were not included, such that each bird had at most a single capture per session.

While La Quebrada had the complete time series data (nine years) with its six mistnets, the mistnets were aligned and only minimally separated (Figure 2) making it unsuitable for the calculation of sigma (σ), that is the shape parameter that characterises movement in SCR models (Royle *et al.*, 2014). For this reason, we calculated sigma for the years 2010-2013 at El Morenillo inland station, also in TDNP and 3 km from the La Quebrada, with 13 mistnets (Figure 1 and Figure 2; Supplementary material appendix 1) and the same sampling pattern with a maximum of seven sampling days. The obtained sigma value (mean and standard deviation) was used as informative prior to fitting a model with fixed sigma for La Quebrada (see Supplementary material appendix 2).

Our data allowed us to calculate the total, recruitment and adult populations –as

difference between total and recruitment– but not the female population, because of a low number of recaptures in some years.

The dry and flood phase data were supplied by the TDNP staff according to the following criteria: the dry phase was characterised by the absence of water for least 2km from the mistnet stations, while the flood phase corresponded to the presence of shallow water at the same location during the sampling period. The dry phase was between autumn 2005 to winter 2009 (sampling seasons of 2006, 2007, 2008 and 2009), and the flood phase was before autumn 2005 and since spring 2010 (sampling seasons of 2005, 2010, 2011, 2012 and 2013).

We compared two different models– the null model (M_0) and the model with temporal variation in basal detection (M_t):

$$\lambda_o[t] = \alpha_0 + w_{[1]} \times \alpha_2 \times Time[t]$$

For model selection, we used the Kuo & Mallick indicator variable selection approach to select the best candidate model in relation to the use of different parameters in the models (Kuo & Mallick, 1998). We use a new binary variable $w[1]$ to evaluate the relevance of each covariate in terms of improving the model (See Supplementary material appendix 2). If $p(w[1])$ is close to 1, it provides strong evidence that a given covariate improves the model. If $p(w[1])$ is close to 0, it should not be used.

All models were run in Nimble 0.6-7 (See Supporting Information) in R (R Core Team, 2017). We ran three chains of the MCMC sampler with 50,000 iterations in each case. To check for chain convergence, we assessed MCMC convergence and mixing by visually inspecting trace plots for each monitored parameter, and we calculated the Gelman-Rubin statistic R-hat using the R package coda (Plummer *et al.*, 2006) where values below 1.1 indicated convergence. For all parameters in our models, R-hat was always

<1.1. Each model took ten days to run on a desktop Intel® Core™ i7-6700 CPU 3.4GHz, 64 Gb RAM.

RESULTS

The total capture events ranged from a maximum of 134 (76 individuals) in 2005 to a minimum of 14 (12 individuals) in 2009 (see Supplementary material appendix 2).

The sigma value (at a real scale) obtained in El Morenillo was $\sigma = 68.8$ (SD: 6.9) metres using 386 events (see Supplementary material appendix 1). The radius around the activity centre at which detection occurs with 95% probability was 168.38 metres.

The selected models were M_t. The result of the Kuo & Mallick indicator variable was $w[1] = 1$ (see Supplementary material appendix 2). There was a positive temporal trend in basal detection probability (λ_0) throughout the sampling period.

The Reed-warbler total density (individual/ha) estimate in La Quebrada (Table 1) ranged from a minimum in 2009, four years after the dry phase, of 4.52 (SD: 1.27) to a maximum in 2005 (the flood phase) of 24.32 (SD: 3.41). Adult density ranged from a minimum of 0.79 (SD: 0.36) in 2010 to a maximum of 4.40 (SD: 1.18) in 2006 (Table, Figure 3 and Supplementary material appendix 1 & 2).

TABLE 1

Posterior summary statistics for the Common Reed-warbler population during 2005-2013 estimates from the independent multinomial encounter process in a spatial Jolly-Seber model. The mean and standard deviation values of the density (individuals/ha) of the Common Reed-warbler at the Tablas de Daimiel National Park, as well as the 95%. Bayesian credible interval (ICB95%) are shown. Shaded cells denote flooded years, and dry years are unshaded.
[Resumen de estadísticos a posteriori para la población el carricero común en el período 2005-2013 estimados con un modelo espacial Jolly-Seber bajo un proceso de encuentros multinomial. Se muestran los valores de la media y desviación estándar de la densidad (en individuos por hectárea) así como el intervalo de credibilidad bayesiano del 95%. Las celdas en sombreado señalan los años con inundación, y los años secos están sin sombrear.]

Year	TOTAL				Adults				Recruitment			
	mean	sd	ICB95%		mean	sd	ICB95%		mean	sd	ICB95%	
2005	24.32	3.41	18.46	31.71								
2006	18.34	2.88	13.40	24.68	4.40	1.18	2.49	7.03	13.97	2.62	9.37	19.63
2007	17.33	3.07	12.08	24.09	3.29	0.98	1.68	5.49	14.06	2.85	9.15	20.36
2008	8.42	1.88	5.27	12.67	2.96	0.97	1.39	5.20	5.47	1.80	2.34	9.45
2009	4.52	1.27	2.49	7.40	1.50	0.00	0.60	2.78	3.03	1.24	1.03	5.79
2010	6.81	1.53	4.32	10.25	0.79	0.36	0.22	1.61	6.04	1.49	3.52	9.37
2011	9.53	1.88	6.37	13.69	1.08	0.46	0.37	2.12	8.47	1.82	5.42	12.52
2012	8.58	1.63	5.79	12.23	1.58	0.58	0.66	2.93	7.00	1.56	4.32	10.40
2013	14.87	2.60	10.47	20.65	1.37	0.53	0.51	2.56	13.52	2.50	9.30	19.04

Discussion

Methodological aspects

The methodological approach used in this study –a spatial Jolly-Seber model– allowed us to compare not only different study sites, but also between years, obtaining comparable density estimate results. Moreover, the use of SCR-Jolly Seber enabled us to obtain the recruitment occurring across time, also expressed in density values.

One of our study's potential shortcomings is the spatial scope of population response. We could not delimit quantitatively *a priori* the fraction of the local population using alternative locations or not breeding, and how these factors influence the regional population results. On the other hand, it was not possible to directly evaluate immigration and emigration rates. However, this last potential difficulty was minimised by analysing only the nesting fraction of the population during the breeding period –when the presence in a given area of the adult birds can be considered as stable due to their territorial behaviour (Newton, 1992)– and, for juvenile birds, before migratory movements began (Chernetsov and Titov, 2001; Jakubas and Wojczulanis-Jakubas, 2010).

It would have been desirable to have deployed other nets at La Quebrada in a configuration that would allowed the calculation of sigma. In our study, we used the sigma value as a prior calculation involving the same species in the same area, but in a different location (El Morenillo) and only during a flood phase. If the ultimate determinant of both density and home-range size is the availability of food or other resources, we can expect, according to Efford *et al.* (2016), that the value of sigma would increase in the poorest habitat. In this case, we may have overestimated the population in less productive years. Despite this possible bias, which could accentuate the differences, the calculations and conclusions are adequate.

Constant-effort mistnet stations can provide enough information to run capture-recapture approaches and to detect small changes and tendencies in the studied populations, although a prerequisite is that they are able to capture the movements of target species (sigma estimates). For small passerines, an appropriate design is a "U" layout with at least 100m of nets located 30m apart, with the mistnet centres ranging between σ and 2σ (Sun *et al.*, 2014). Such a design would have allowed a better adjustment of the sampled data, for example by using models including sigma variation between years. Otherwise, a sampling design as described by Ergon & Gardner (2013) and Schaub & Royle (2014), together with the methods (also spatially explicit) from the same authors, would generate a more detailed demographic description, separating mortality/emigration and birth/immigration.

Population and conservation implications

The population size estimates obtained in our study (adults per hectare) are in the lowest range reported by other authors. Dyrcz *et al.* (2018), in a compilation of different studies, cited 6.5-21.6 breeding pairs/ha. It is possible that differences across studies result from different analytical approaches, from the contrasting sizes of the study areas where densities were calculated, and especially, from possible differences in habitat quality for the Common Reed-warbler from those at our study site.

The analysis of events that occurred in between 2005-2013 are indicative of how Mediterranean wetlands may evolve in a future scenario of climate change, where an increase in temperature, decrease in rainfall and exacerbation of water fluctuations in seasonal wetlands will cause a decrease in the hydroperiod and a consequent reduction in food availability (Frampton *et al.*, 2000; Chernetsov & Manukyan, 1999). Lande *et al.*

(2003) indicate that stochastic environmental fluctuations are an important risk factor for populations, even driving some populations to the verge of extirpation. Drought in the TDNP was an extreme and anomalous form of environmental stochasticity. Here, the response of the Common Reed-warbler to the drought was a modification of productivity, matching greater productivity values to flooding periods, albeit with a time lag. This productivity-drought pattern is similar to that indicated by Sæther *et al*. (2016), who found that environmental stochasticity simultaneously impacted all vital rates, but most strongly the temporal variation in the number of new recruits entering the population. Nevertheless, the response of wetlands to climate change would be the opposite to that described in northern latitudes (Halupka *et al*., 2008).

We found that the probability that the Reed-warblers reproduce successfully in a given year is a function of habitat quality, but also seems to be influenced by breeding success in the previous year (Schaub *et al*., 2011). However, in our case study, the response of non-recruitment is progressive, with recruitment continuing until it stopped completely four years after the beginning of the drying process. After reflooding, the recruitment response also shows a lag, suggesting an interaction between the number of years from drying and flooding in the previous year.

Recruitment under drying conditions, and its reduction over time, may be an adaptation to the seasonality of Mediterranean wetlands. Thus, the Common Reed-warbler would be able to cope with environmental stochasticity in this system. However, if dry phase periods become longer, we can expect that this palustrine population will become extremely vulnerable on a regional scale. Such a negative effect due to long-term droughts could affect other Mediterranean marsh-dwelling birds that are more threatened than the Common Reed-warbler, such as the Moustached Warbler *Acrocephalus melanopogon* and the Reed Bunting *Emberiza schoeniclus witherbyi*
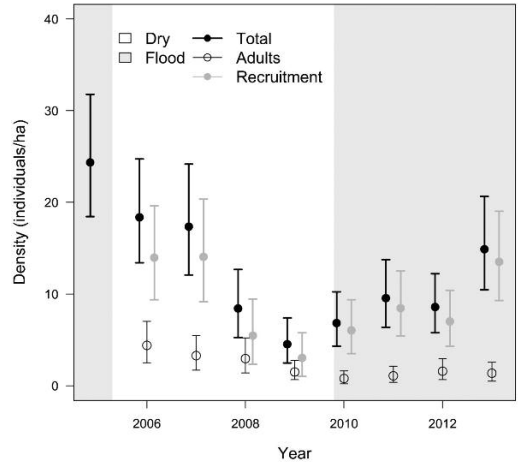

FIG. 3.—Density evolution of adults, total population and recruitment of Common Reed-warblers *Acrocephalus scirpaceus* during 2005-2013, in La Quebrada when flooded (grey) and dry (white). Mean values and 95% Bayesian credible interval are shown.
[Evolución de la densidad de los adultos, población total y reclutamiento del carricero común Acrocephalus scirpaceus *en el período 2005-2013, en La Quebrada en situación de inundación (en gris) y seco (blanco). Se muestran los valores medios y el intervalo de credibilidad bayesiano del 95%.]*

that preferentially select continually inundated habitats (Jiménez *et al.,* 2015). Therefore, and despite the described potential adaptive mechanisms to particular ecological conditions in their breeding areas, a reduction in the biodiversity of specialised species within flooded Mediterranean environments may be expected if drought periods become longer in the long term (Filipe *et al*., 2013). This progressive reduction in population sizes could be reflected through a progressive reduction in observed recruitment.

Conclusions

The main contributions of our study are twofold. The first is related to the application

of new analytical methods of data collected in long-term monitoring programs that use bird sampling and individual marking. Using spatially explicit capture-recapture systems, population densities can be accurately calculated. However, the distribution of the detectors (in our case, mist nets) needs to be properly spaced with a distance between them enabling spatial recaptures and calculation of the movements of individuals.

The second contribution is related to the ecological consequences of prolonged periods of drought affecting freshwater wetland conservation in the Mediterranean basin. Marsh-dwelling birds and other specialised organisms are sensitive to environmental changes in these wetlands which are consequently reflected in their demography. Despite showing some plasticity and resilience to changes in habitat traits –shown by the shifts in population density occurring only after several years of continuous drought or reflooding (Figure 3)–, density, and recruitment and productivity rates of marsh bird communities may be severely affected if habitat alteration persists long term (Filipe *et al.*, 2013). It could even lead to local extinction, especially of the rarest or most threatened species (Cahill *et al.*, 2013). The observed trend of global change due to climate change and the abuse of water resources by humans are the most probable causes reducing biodiversity in inland Mediterranean wetlands with periodic or permanent flooding (Kingsford *et al.*, 2016).

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SUPPLEMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the on-line version of this paper. See volume 65(2) on www.ardeola.org.

Appendix 1. R+BUGS code and data from Common Reed-warbler in El Morenillo (Tablas de Daimiel National Park) 2010-2013 for sigma calculation.

Appendix 2. R+BUGS code and data from Common Reed-warbler in La Quebrada (Tablas de Daimiel National Park) 2005-2013.

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