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Research Paper

Population trends and habitat selection of threatened marsh passerines in a protected Mediterranean wetland

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ABSTRACT. Many marsh passerines are cataloged as threatened taxa, mostly due to their high degree of specialization and the generalized deterioration of wetlands worldwide. In this context, habitat selection studies are a very helpful tool to achieve optimal wetland management, take appropriate conservation measures, and avoid potential conservation conflicts resulting from species-specific habitat requirements. For this purpose, we analyzed the population trends and habitat requirements of the threatened marsh passerine community inhabiting a protected Mediterranean wetland with persistent hydrological problems due to aquifer overexploitation. Listening points were conducted yearly for eight consecutive years (2012-2019), and habitat categorization and abundance estimation of the target species (Great Reed Warbler, *Acrocephalus arundinaceus*; Moustached Warbler, *Acrocephalus melanopogon*; Reed Bunting, *Emberiza schoeniclus witherbyi*; Savi's Warbler, *Locustella luscinioides*; Bearded Tit, *Panurus biarmicus*) were performed at each point. Our results show that the populations of the Great Reed Warbler strongly declined during the study period while those of the Reed Bunting increased; the remaining species experienced an initial increase in abundance but have declined in recent years. The habitat type, measured as relative cover of common reed, saw sedge, bulrush, dry vegetation, open water, and dry surface was important to explain variations in the marsh passerine community structure. Focal species showed different, and even opposite, habitat requirements over the course of eight years, but the abundance of all species seem to be conditioned by disturbances in the wetland water regime. Conservation implications, including the importance of wetland hydrological regime and the presence of heterogeneous environments, are discussed in order to provide relevant information for the conservation of the marsh passerine communities of Mediterranean wetlands.

Les tendances de la population et la sélection des habitats des passereaux des marais menacés dans un milieu humide méditerranéen protégé

RÉSUMÉ. De nombreux passereaux des marais sont catalogués comme des espèces menacées, principalement en raison de leur degré de spécialisation élevé et de la détérioration généralisée des zones humides dans le monde entier. Dans ce contexte, les études sur la sélection de l'habitat constituent un outil précieux pour parvenir à une gestion optimale des zones humides, prendre des mesures de conservation appropriées et éviter les conflits potentiels de conservation résultant des exigences d'un habitat spécifique à une espèce. À cette fin, nous avons analysé les tendances des populations et les exigences d'habitat de la communauté de passereaux des marais menacée habitant une zone humide méditerranéenne protégée connaissant des problèmes hydrologiques persistants dus à la surexploitation des aquifères. Des points d'écoute ont été mis en place chaque année pendant huit années consécutives (2012-2019) et la catégorisation des habitats et l'estimation de l'abondance des espèces ciblées (Rousserolle turdoïde, *Acrocephalus arundinaceus*; Lusciniolle à moustaches, *Acrocephalus melanopogon*; Bruant des roseaux, *Emberiza schoeniclus witherbyi*; Locustelle lusciniolide, *Locustella luscinioides*; Panure à moustaches, *Panurus biarmicus*) a été réalisée sur chaque point. Nos résultats indiquent que les populations de rousserolles turdoïdes ont fortement décliné pendant la période de l'étude, alors que celles de bruant des roseaux ont augmenté; les autres espèces ont connu une augmentation initiale de leur population, laquelle a ensuite décliné au cours des dernières années. Le type d'habitat, mesuré en tant que couverture relative de roseaux communs, de carex, de joncs, de végétation sèche, de pièces d'eau et de surfaces sèches, était important pour expliquer les variations de la structure des communautés de passereaux des marais. Les espèces observées ont présenté des exigences différentes, voire opposées en termes d'habitat au fil des huit années considérées, mais l'abondance de toutes les espèces semble être conditionnée par les perturbations du régime hydrologique des marais. Les implications pour la conservation, y compris l'importance du régime hydrologique des marais et la présence d'environnements hétérogènes, sont discutées afin de fournir des informations pertinentes pour la conservation des communautés de passereaux des marais des zones humides méditerranéennes.

Key Words: *bird conservation; habitat requirements; marsh passerines; water management; wetland.*

INTRODUCTION

A wide variety of taxonomic groups depend on the conservation of the wetlands that harbour them (Gibbs 2000, Quesnelle et al. 2013). The widespread deterioration of wetlands around the world has had a negative effect on the associated bird communities (Ma et al. 2010, Maclean et al. 2013) resulting in a decrease in species richness and abundance and is especially detrimental to scarcer species (Finlayson et al. 1992, Parsons et al. 2002, Paracuellos 2008). Among these birds are the marsh passerines, a polyphyletic group that, due to its high degree of specialization and dependence on the conservation of wetlands, has a large number of severely threatened species (Tanneberger et al. 2009, Trnka et al. 2014).

Marsh passerines have species-specific preferences for different wetland habitats, including the plant community and its spatial structure as well as the area of flooded surface (Báldi and Kisbenedek 1999, Poulin et al. 2002, Martínez-Vilalta et al. 2002). These interspecific differences mean that management techniques applied in wetlands may affect the abundance of each species in different and even opposite ways, which can potentially create conflicts over the conservation of several threatened species (Mitchell et al. 2006, Ma et al. 2010). For example, winter cutting of reed beds causes a decrease in the abundance of some species that do not find suitable nesting sites in the cut areas (Poulin and Lefebvre 2002), but in contrast, this technique does not seem to negatively affect, and may even benefit, the populations of other species (Vadász et al. 2008, Tanneberger et al. 2009). Actually, wetland management is rarely focused entirely on biodiversity conservation, which is often in conflict with other socio-economic factors (Birol et al., 2009, Downard et al. 2014) given the wide diversity of resources and ecosystem services provided by wetlands (Zedler and Kercher 2005, De Groot et al. 2012). Taking this issue into account, studies on habitat requirements of marsh birds are needed to achieve optimal wetland management and take appropriate conservation measures (Milsom et al. 2000, Poulin et al. 2002, Smart et al. 2006).

The National Park and Biosphere Reserve of Tablas de Daimiel (Spain) is one of the most important wetlands on the Iberian Peninsula for the conservation of many marsh passerines. Despite being protected, this wetland has suffered great disturbances in its hydrologic regime during the past decades as a result of human activities (Álvarez-Cobelas et al. 2001, Sánchez-Carrillo et al. 2016). This has led to artificial water management in the park to ensure there is a minimum flooded area. Water transfers, the creation of three dams, and groundwater pumping from emergency wells are some of the measures taken for this purpose, although they appear to have limited effectiveness (Sánchez-Carrillo and Álvarez-Cobelas 2010, Aguilera et al. 2013). The overexploitation of the aquifer for agriculture continues to cause an alarming reduction in the wetland hydroperiod and the area of flooded surface (Llamas 1988, Álvarez-Cobelas et al. 2001), reaching critical situations such as the one that occurred in 2009 when the aquifer dried out completely and ignited by self-combustion (Moreno et al. 2010, Aguilera et al. 2013). These large fluctuations in water level can have negative impacts on the populations of threatened marsh passerines that breed in this area (Desgranges et al. 2006, Sánchez-Carrillo and Angeler 2010). In addition, variations in the water regime have caused significant

changes in its plant community (Álvarez-Cobelas et al. 2001, Sánchez-Carrillo et al. 2016) resulting in a shift in the availability of suitable habitats for passerines (Poulin et al. 2002, Báldi 2005, Jiménez et al. 2015) that affects the abundance and potential recovery of populations of endangered species.

We analyzed the effect of water regime variation in the protected wetland of Tablas de Daimiel over the past decade on threatened marsh passerines to understand how water management can influence their conservation. Our hypotheses, based on previous studies, suggest that (1) problems in the water regime of the wetland may affect the population trends of the marsh passerines breeding in the national park. Although we expect (2) differences in the population trends of the study species due to (3) the differences of species-specific habitat requirements, and (4) declining water levels result in the disappearance of suitable habitats for some species and their populations will consequently be affected in a negative way.

METHODS

Study area and focal species

The National Park of Tablas de Daimiel (Ciudad Real, Spain, 39° 08' 36" N, 03° 42' 18" W, 606 m a.s.l.), is one of the largest continental wetlands in the Iberian Peninsula (up to 1800 ha of flooded surface) and part of the Mancha Húmeda Biosphere Reserve (Fig. 1). The water regime of the wetland depends on the confluence of the Cigüela River with the discharge zone of the La Mancha Occidental aquifer (5500 km²), located in the Guadiana River Basin. Historically, the flooded area was maintained mainly by the discharge of the aquifer, but due to its over-exploitation, the wetland may at present even act as a recharge zone (Aguilera et al. 2013). This may lead to hydrological crises such as the one that occurred in 2006 when there was a severe drought eventually leading to the total desiccation of the wetland in 2009. In 2010, however, the park recovered its entire flooded area due to the discharge of the aquifer caused by the significant rise of the phreatic level that occurred after a large amount of rain during that year.

During the period of study (2012-2019) the flooded area of the wetland fluctuated strongly depending on the amount of groundwater reaching it from the Guadiana river basin. The general trend in the size of flooded area over the years was negative: $y = -110.48 \pm 223996.01$, $t = -3.15$, $R^2 = 0.56$, $P = 0.02$ (Linear Regression model was conducted from the total flooded area data, in hectares, of the national park on the first weekend of May each year). Although in the first years the flooded surface was near its maximum, the flooded surface drastically declined throughout the last five years of the study and in the last year (2019) only 675 hectares were flooded, which is equivalent to a third of the total capacity of the wetland.

The wetland plant community is characterized by large areas of helophytic flora. The common reed (*Phragmites australis*) is the dominant species and it usually covers large monospecific areas. There are also patches of other species such as bulrush (*Typha domingensis*) or saw sedge (*Cladium mariscus*). In the driest areas, where the surface is not permanently flooded, grasslands predominate and the tamarisks (*Tamarix canariensis* and *Tamarix gallica*) constitute the arboreal strata.

Fig. 1. Distribution map of the listening points and census routes carried out each year in the National Park of Tablas de Daimiel (bold continuous line: external limits of the park). Source of cartographic material: © Ministerio para la Transición Ecológica y el Reto Demográfico.

The target species of this study were the Great Reed Warbler (*Acrocephalus arundinaceus*), the Moustached Warbler (*Acrocephalus melanopogon*), the Reed Bunting (*Emberiza schoeniclus witherbyi*), the Savi's Warbler (*Locustella luscinioides*), and the Bearded Tit (*Panurus biarmicus*). The criteria used for the selection of these species were that (1) the species were included in the Spanish Catalogue of Threatened Species and other national inventories of threatened fauna, (2) their population size in this wetland was important for the viability of this species in a regional and/or national context (e.g. Madroño et al. 2004, Monrós et al. 2018), and (3) that there was evidence of differences in the habitat requirements of the selected species (e.g. Martínez-Vilalta et al. 2002).

Bird sampling and habitat characterization

With the aim of estimating the population size and habitat selection preferences of the focal species, listening point censuses (Bibby et al. 1992) were carried out during the first weeks of May (based on the reproductive phenology of these birds) for 8 consecutive years, starting in 2012. Each year more than a hundred listening points were established over two consecutive days. We restricted sampling to the first and last three hours of the day when the peak of activity occurs and therefore it is easier to detect these species.

Prior to the censuses, the wetland was divided into several routes, which would be repeated every year, in order to cover the maximum surface area and the widest representation of habitats possible (Fig. 1). Five-minute listening points were established

every 300 m of the route, and once each point was completed, the number of individuals of each target species detected was recorded. The number of listening points varied slightly between years due to issues related to the wetland conditions (such as changes in accessibility to certain areas due to changes in the flooded surface or the cover of marsh vegetation). We checked that such small variation produced no major effects on the number of detected individuals in other years.

Special attention was given to the census of the Reed Bunting. During the 5 minute sampling period, a recording of the territorial song of a male was played twice for one minute, followed by one minute of silence, resulting in the sequence: silence-playback-silence-playback-silence. This methodology was used according to the methodology of the Spanish national census for the species (Atienza 2006), because this species requires such a specific protocol (which does not affect the detection of the other species) in order to obtain a precise population estimate, which is of vital importance due to the critical situation that the taxon is going through.

Imperfect detection was taken into account when creating the census design. Target species detection was maximized by carrying out the censuses in the first and last 3 hours of the day in early May, in accordance with suggestions in the detection probability study carried out by Jimenez et al (2015) in the Tablas de Daimiel National Park with 3 of the 5 species in the study. These conditions were the reason for concentrating the greater part of the sampling effort (~130 listening points in an area of approximately 1800 hectares) in only two consecutive days.

Census methodology for the Reed Bunting was also different from the others as it seems that this species is mostly detected visually, unlike other species that are easily detected by their song (Moskát and Báldi 1999, Jimenez et al 2015).

In addition, a characterization of the habitat was made at each listening point. To do this, we recorded the percent cover of each of six categories within a radius of 25 meters around the listening point. Four categories referred to vegetation type, including three dominated by the species *Cladium mariscus*, *Phragmites australis*, and *Typha domingensis* and a non-specific category called "DrierVeg", which included vegetation characteristic of non-floodable zones within the wetland, such as *Tamarix* sp. or grasses. The remaining two categories corresponded to either "OpenWater" or "DrySurface" within the floodable zone (i.e. bare mud).

Statistical analyses

Population trends of the different species were determined with Generalised Additive Models (GAMs) using the abundance detected of each species at each listening point in the different study years (Fewster et al. 2000). Models were constructed with the "gam" function of the mgcv package (Wood 2016). GAM models have previously been used to assess the long-term population trends of a wide range of bird groups, including waterbirds (Fewster et al 2000, Clarke et al 2003, Atkinson et al 2006).

To identify habitat requirements and to check which variables may play a stronger effect on the abundance of each species, we used Generalized Linear Mixed Models (GLMM), with a negative binomial distribution of the response variable and a log-link function. The cover of *Cladium mariscus* (saw sedge), *Phragmites australis* (common reed), *Typha domingensis* (bulrush), "DrierVeg", "OpenWater" and "DrySurface" were used as fixed effect variables in the models, as they were the main habitat elements found in the wetland and have been used in previous similar studies (Martínez-Vilalta et al. 2002, Poulin et al. 2002, Vera et al. 2011). The total flooded area ("TFloodedArea") of the wetland of the corresponding sampling year, was incorporated into the models as a random variable. Collinearity was tested prior to analysis, but no variable was discarded since no high degree of correlation was detected between the studied variables ($R < 0.7$) (Dormann et al. 2013). These models were constructed in R 3.5.2 (R Core Team 2018) with the function "glmer.nb" of the lme4 package (Bates et al. 2015).

The best models resulting from the combination of variables were automatically selected according to the Akaike Information Criterion (AIC) using the "dredge" function of the MuMIn package (Barton 2020). For each species, the best model and those that did not exceed the lowest AIC value by two units were considered, and the weight (w) value was taken into account to calculate the relative importance of each of the variables (RIV) in the set of selected models (Burnham and Anderson, 2002). Finally, the function "tab_models" of the sjPlot package (Lüdtke et al. 2020) was used to obtain the descriptors for each of the selected models, including the R_M^2 and R_C^2 values to show the percentage of the model variance that is explained by the fixed effect variables and the random effect variables (Bates et al. 2015, Mestre et al. 2019).

To obtain an overall view of the relationships between the studied marsh passerines and between the available habitat types through time, we used the constrained ordination technique of Redundancy Analysis (RDA), which allows relating species assemblages to environmental gradients (Legendre and Legendre 2012). RDA was performed with the software Canoco5 (ter Braak and Šmilauer 2012).

RESULTS

Habitat availability

The surveyed areas of the National Park of Tablas de Daimiel were mostly dominated by open water (Fig. 2). Open water was greatest in 2014, when it represented around 50% of the sampled wetland area, but declined as the years passed, along with the decrease in the total flooded area. Decline in water levels caused the appearance of dry surfaces within the usually flooded area ($\approx 18\%$ of the surface) during the last year.

Fig. 2. Mean ($\pm$ standard error) relative cover by each habitat type in the area during the study period.

As for vegetation, common reed was the dominant species in the wetland. It showed maximum extension values of around 40% of the sampled area at the beginning of the study period and decreased slightly in recent years. The area covered by bulrush was small at the beginning of the study period ($\approx 10\%$) but increased over the years, although with large fluctuations, at times occupying up to 25% of the sampled area. The amount of saw sedge remained relatively constant at cover values close to 5% during the study period. Finally, the areas occupied by vegetation of non-flooded zones increased considerably in recent years after the initial drop at the beginning of the study.

Population trends

The studied species experienced distinct and even opposite population trends during the period from 2012 to 2019 (Fig. 3).

The Great Reed Warbler was the only species with a substantial population size at the beginning of the study period. Its population peaked in 2013 with an average of 1.56 individuals per point count (ind./point) detected. The species experienced a severe population decline of 90% in 2019 when the mean number of Great Reed Warblers per point was 0.14. In contrast, the Reed Bunting started from a very low number of individuals (0.10 ind./point) and its populations progressively increased until 2019, quadrupling its population in 8 years (0.39 ind./point).

Fig. 3. GAM smoothing curves fitted to variation in population size of the different species during the study period. Shaded areas correspond to confidence intervals (standard error). Y-axis label indicates the degree of smoothing (degrees of freedom for non-linear fits).

The Moustached Warbler and the Savi's Warbler had similar population trends throughout the study period. Starting from a low number of individuals, especially for the Moustached Warbler (0.03 ind./point), both species experienced a considerable population increase until 2014, when the population growth stopped. Between 2014 and 2016 there was a two-year period of stability in the Savi's Warbler populations and of population decline in the Moustached Warbler, preceding a new period of increase until 2018. In that year there is again a change in the population trend and the populations of both species fall considerably (from 0.40 to 0.10 ind./point in the Moustached Warbler and from 0.94 to 0.79 ind./point in Savi's Warbler).

Finally, the Bearded Tit had strong population growth until 2017 (from 0.23 to 2.06 ind./point) when the trend changed drastically and it suffered a sharp decline that reduced the number of individuals by more than 50% (0.86 ind./point in 2019).

Habitat selection

The results obtained indicate that the Moustached Warbler, Savi's Warbler and Bearded Tit avoided vegetation from non-floodable areas within the wetland such as grasslands and tamarisk formations (RIV=1). This habitat element, however, does not seem to have had a major influence on the presence of Reed Bunting (RIV=0.5) and Great Reed Warbler (RIV=0.38) populations (Table A1.1, Fig. 4).

Fig. 4. Mean $\pm$ SD of the coefficients obtained for each of the six habitat variables studied in the best GLMM models selected for each bird species. C (%Cladium), P (%Phragmites), T (%Typha), DV (%DrierVeg), OW (%OpenWater), DS (%DrySurface).

The Reed Bunting was underrepresented in habitat dominated by large bulrush coverage but benefited from the presence of saw sedge formations (Table A1.1, Fig. 4). High reed cover, on the other hand, seemed to negatively affect the Moustached Warbler (Table A1.1, Fig. 4, Fig. 5). For this species, the proportion of saw sedge was also generally higher in used than in available habitat, but this relationship was weaker than in the previous case, with a RIV= 0.55 in the GLMMs. Saw sedge, in addition, also seems to have a positive effect on Savi's Warbler numbers (Fig. 4, Table A1.1).

Fig. 5. Ordination graph of a Redundancy Analysis (RDA) showing the relationship between the variables measured (red arrows) and the abundance of the study species (blue arrows).

The Bearded Tit, besides avoiding areas with non-floodable vegetation, also avoided the dry areas of the floodable zone of the wetland resulting from the decrease in water surface during the last study year. These dry surfaces, on the other hand, appeared to be used by the Reed Bunting (Table A1.1, Fig. 4).

The amount of open water was an important habitat element for every species' abundance, generally affecting positively except for Moustached Warbler, which apparently avoided this kind of habitat.

For the Great Reed Warbler the R_M^2 value represented between 4 and 11% of the R_C^2 value obtained in the best GLMMs (Table A1.1), so the fixed effect variables considered explained a very small proportion of the variance of this species compared to the random variable (total flooded area). In contrast, for the Moustached Warbler, Savi's Warbler and Bearded Tits, R_M^2 accounted for 70-80% of the total variance explained by the models, suggesting a greater strength of the fixed effect variables on the abundance of these species. For the Reed Bunting, with R_M^2 representing around 55% of R_C^2 , the percentage of variance explained by the fixed and random effects variables was more balanced.

The RDA results (Fig. 5) indicate a strong relationship between the Great Reed Warbler population variability and total flooded area of the wetland, so as the negative effects of time progression (Year) on the species populations. The other species were all ordered on the opposite part of axis 1. In addition, the Reed Bunting was ordered on the positive part of axis 2 since its populations increased with time and benefited from the presence of saw sedge and dry surfaces in the floodable zone. The Bearded Tit, on the other hand, was ordered on the extreme negative part of axis 2, due to the strong negative effect that dry areas and non-floodable zones had on its populations, and the positive effect of open water surfaces on this species, in agreement with the GLMM results. Finally, Savi's and Moustached Warbler remained in the intermediate part of axis 2, apparently negatively affected by the presence of non-floodable vegetation type and large reed extensions (although this was not entirely corroborated by the other analysis).

DISCUSSION

Habitat requirements of the Tablas de Daimiel's marsh passerines

Our results, in agreement with similar studies carried out in other locations, show that the different species that form the marsh passerine community of Tablas de Daimiel have species-specific habitat requirements (Poulin et al. 2002, Martínez-Vilalta et al. 2002, Trnka and Prokop 2006, Jiménez et al. 2015).

The total flooded surface area of the wetland was the most important variable explaining the abundance of the Great Reed Warbler. Widely flooded areas, especially with certain fluctuation of water levels, promote insect population explosions and the development of reeds with optimal stem thickness that allow the Great Reed Warbler to perch and build its nests (Jedraszko-Dabrowska 1992; Graveland 1998, Poulin et al. 2002). More flooded area in the wetland leads to a greater amount of available open water which was positively related to Great Reed Warbler

abundances, according to the GLMM results. This is in agreement with previous studies showing that this species is present at higher densities near the vegetation edges, especially in reed bed formations close to free water, where it also builds its nests (Rolando and Palestrini 1989, Graveland 1998, Prokešová and Kocian 2004, Trnka et al. 2009). Despite the large number of studies that conclude that there is a close relationship between this species and reeds (Rolando and Palestrini 1989, Martínez-Villalta et al. 2002, Méro et al. 2015), our results do not show a special preference by this species for reed over open water flooded areas. This may be indicating that the condition of reed plants, such as thickness, height or stem density, which depend upon flooding levels (Graveland 1998), might be more important for the Great Reed Warbler than the amount of reed cover itself. Finally, despite the strong dependence on the flooded surface found, our results indicate that Great Reed Warbler did not avoid dry vegetation from non-floodable areas within the wetland, as other species did. This may be because a large part of the wetland population of this species can be found in the south-western part of the national park, where the flooded surface and aquatic vegetation are very close to the boundary roads where grasslands and tamarisks are common, and where the Great Reed Warblers can occasionally be detected.

Our results show a clear positive relationship between the Reed Bunting and saw sedge formations, in agreement with previous surveys (Martínez-Villalta et al. 2002, Bigas and Copete 2004, Vera et al. 2009, Jiménez et al. 2015). The presence of dry, unvegetated surfaces in the wetland floodplain also favored its populations. This seems to be related to the way the Reed Bunting feeds and moves; in addition to climbing through the marsh vegetation, it frequently moves on the ground (Martínez-Villalta et al. 2002). Vera et al. (2011, 2014) found the presence of bulrush patches, rather than saw sedge, was a determining factor in the distribution of this Reed Bunting subspecies in Spanish wetlands (Vera et al. 2011, 2014). However, we found they seemed to avoid that vegetation type. These contradictory results could be explained by the difference in the scale of analysis of both studies. Vera et al.'s (2011) study was at a wetland scale within the distribution area of the species while our research was conducted at a microhabitat scale within the wetland. Perhaps the presence of bulrush patches is indicative of some feature of the wetland that favors the presence of the species in that particular locality, but on a smaller scale, Reed Buntings preferentially use saw sedge instead of bulrush formations.

Previous studies on the habitat requirements of Moustached Warbler's Spanish populations, including Tablas de Daimiel, indicate that the species avoids large monospecific reed extensions (Martínez-Villalta et al. 2002, Castany and López 2005) and favors other helophytes that are more sensitive to fluctuations in the water level such as saw sedge (Jiménez et al., 2015). Our results support these conclusions, indicating a negative effect of high reed cover on the presence of the species and a positive effect, though weaker than in the previous case, of the saw sedge formations. Due to their nesting and feeding habits, it has been found that this marsh passerine inhabits areas close to flooded surfaces (Bibby 1982, Fessl and Hoi 1996, Trnka and Prokop 2006), in agreement with the negative effects of dry vegetation on its abundance in our study. The GLMM results, however, indicated that open water surfaces negatively affected the abundance of the

species. The Moustached Warbler builds its nests at the base of the helophytic vegetation (0-0.5m), much lower than other species such as the Great Reed Warbler (Leisler 1991a, b). The large fluctuations in the water levels of the wetland during the study period, which could facilitate predation or cause flooding of the nests, could be reasons why this species avoided the low areas near wide open water surfaces and perhaps preferred small, more sheltered, waterlogged areas.

The Savi's Warbler, like the Reed Bunting and Moustached Warbler, showed a preference for habitats with high cover values of saw sedge. The same results were found by Martínez-Villalta et al. (2002) in the Ebro Delta (Spain). This preference, however, varies across its geographical distribution, suggesting that the structure formed by vegetation, specifically the presence of an extensive basal stratum of straw litter, is more important than the plant species itself (Neto 2006, Bergner and Gezelius 2013). This preference has been suggested to be related to its mode of foraging near water surfaces (Bibby and Lunn 1982, Bergner and Gezelius 2013), which in turn agrees with our results on the positive effects of open water on the abundance of this species. The preference of the species for areas with saw sedge, a vegetation type of flooded areas with reduced fluctuations, and for open water areas, is supported by the negative effects of dry terrestrial vegetation on the abundance of the species found in our study. In contrast, other authors conclude that the species has a preference for dry areas where it also feeds (Martínez-Villalta et al 2002, Trnka and Prokop 2006).

Bearded Tits were absent in the driest areas of the wetland, where bare mud and vegetation of non-floodable surfaces appeared, while their abundances increased in open flooded areas. Dependence on open water by the Bearded Tit has been previously recorded and explained by its feeding and nesting mode (Bibby and Lunn 1982, Poulin et al. 2002, Brichetti and Grattini 2008). Despite this apparent dependence of the species on flooded areas, no relation was found between the total flooded area of the park and the abundance of the Bearded Tit. This may be the result of a temporary mismatch derived from the small initial population size, caused by the water crisis in the previous years and the sudden recovery of the total flooded area of the wetland in only one year. Adverse climatic conditions during particularly severe winters, such as heavy flooding, can have a significant effect on breeding populations of this species (Campbell et al 1996, Wilson and Peach 2006). Thus, the large floods recorded in the wetland in late 2010, together with other factors such as the absence of suitable habitat in previous years, could be responsible for the Bearded Tit's small initial population size. Furthermore, no vegetation type was selected by the species in the study period, in agreement with the study by Jiménez et al (2015) carried out in Tablas de Daimiel, where they suggested that this species may be more generalist than other sympatric species such as the Reed Bunting and the Moustached Warbler.

Wetland hydrological changes and their effects on the abundance of marsh passerines

Due to the conservation problems associated with the hydrology of this wetland, between 2006 and 2010 the Tablas de Daimiel National Park was completely dry. Under these conditions, the

aquatic vegetation dependent on regular water levels was substantially decimated compared to the reed beds. Open water areas were non-existent and terrestrial vegetation began to replace the helophytic vegetation due to the absence of floods (Sánchez-Carrillo et al 2016). These transformations in the available habitat may have been responsible for the small population size of most species at the beginning of the study period according to our results, and as has been observed in other marsh passerine species in the same wetland (Jiménez et al. 2018).

After a particularly rainy autumn in 2010 and with help from artificial water management, the wetland suddenly recovered its entire flooded surface. The great fluctuations in the water levels caused the reed to benefit over other species of helophytes such as the saw sedge (Sánchez-Carrillo et al 2016) and also to have a considerable stem thickness (Poulin et al 2002). The sudden inundation of the wetland may have had negative effects on the abundance of some marsh passerines as mentioned above, but on the other hand, it also led to the appearance of wide-open water surfaces and to abundance peaks in insects. According to our results and the existing literature (Graveland 1998, Poulin et al. 2002, Prokešová and Kocian 2004), such conditions might have been optimal for the Great Reed Warbler's populations, which at the beginning of the study period presented maximum values of abundance.

The presence of areas with constant water levels led to the appearance of extensions of other helophyte vegetation such as saw sedge and bulrush, which replaced reeds under certain conditions (Álvarez-Cobelas et al. 2001, Jiménez et al. 2015). These changes in the wetland vegetation structure may have benefited the populations of marsh passerines associated with these formations, including Reed Bunting, Moustached Warbler and Savi's Warbler (Martínez-Villalta et al. 2002, Bigas and Copete 2004, Jiménez et al. 2015), which started to become more abundant. Due to the re-flooding, the dry areas and terrestrial vegetation that occupied the inner surface of the wetland disappeared and were occupied by open water, which would in turn, benefit the Bearded Tit populations. All these endangered birds appear to have benefited from the re-establishment of the wetland's water regime and the changes in habitat structure resulting from it. However, as the years went by, the flooded area began to decrease again.

The strong reduction of the flooded surface seems to be the main cause of the sharp population decline suffered by the Great Reed Warbler. Even though some areas remained flooded, the decrease in water levels, especially pronounced between 2017 and 2019, caused the disappearance of wide open water surfaces, the appearance of dry areas, and an increase in terrestrial plant cover within the wetland. Those factors affected the abundance of the Bearded Tit, Moustached Warbler, and Savi's Warbler and can explain population declines observed in the last study years. The population of the Reed Bunting, however, was most likely sustained by saw sedge plasticity, which may continue to grow even when the surface begins to dry out (Sánchez-Carrillo et al 2016) and by the appearance of the dry areas that seem to be used by the species for feeding (Martínez-Villalta et al. 2002).

We took precautions regarding bird detectability through our monitoring design, and after evaluating the data we consider these precautions sufficient to analyze population trends using the

GAM models. Although problems with imperfect detectability can be addressed with statistical analyses that correct for consequential biases (Kéry and Schmidt 2008) to better estimate population abundances of the studied species, to focus conservation efforts on those having reduced densities, further research should take detectability issues into consideration.

Conservation implications

Despite the numerous management strategies applied, the problems associated with the wetland water regime in the Tablas de Daimiel National Park remain unsolved (Sánchez-Carrillo et al 2021). During the study period, the flooded surface of the wetland went from maximum capacity to only a third in 5 years. The consequences on the marsh passerine community were recorded in the later years of the study. If the water level problems are not fixed, the park will dry out entirely again, which will lead to the collapse of the populations of the studied endangered species and many more.

Tablas de Daimiel is one of the most important wetlands at a regional and national level for the conservation of marsh passerines. For instance, in the first national census of the endangered Reed Bunting in 2005, its population in the park was the second largest in Spain, and it has been considered important for the viability of the species (Kvist et al. 2011). However, 10 years after the survey the number of breeding pairs had been reduced by almost 90%. The population increase recorded in the last years of this study is an important change of trend for the conservation of this species (Atienza 2006, Monrós et al. 2018) but if the current situation persists, its populations will fall again due to the disappearance of its suitable habitats (Sánchez-Carrillo et al 2016). Las Tablas de Daimiel is also the most important wetland for the metapopulation of the Bearded Tit in Castilla la Mancha, hosting the main population of this marsh passerine in the Iberian Peninsula due to the small population sizes in the northern wetlands of the region and the dramatic decline suffered in the Mediterranean ones (López-Iborra and Monrós 2004, Belenguer Barrionuevo et al. 2016). Reliable management strategies that would guarantee the viability of the populations in the park are required to ensure the conservation of these species.

The results of the present research highlight the need to ensure the long-term viability of the populations of threatened marsh passerines. Water management should focus on ensuring a minimum flooded area that would allow the development of helophyte vegetation, the availability of open water, and also prevent terrestrial vegetation from spreading over the wetland. The growth of terrestrial vegetation in periods of drought seems to be detrimental to several species in this study, and management by grazing, mowing, and burning seems to be effective solutions to this kind of issue (Vulink et al. 2000, Middleton et al. 2006). In addition, it is recommended that avoiding an excess of stability in the water level to recreate natural fluctuations that allow for explosions of insect populations, the appearance of dry zones, and changes in the composition and structure of the marsh vegetation, will benefit the populations of the passerine species (Poulin et al. 2002, Timmermans et al. 2008, Beemster et al 2010).

When making decisions about which management strategies to adopt, it should be kept in mind that potential conflicts between the conservation of coexisting endangered species may appear as a result of conservation actions focused on individual species. Many factors, such as interactions between species or differences in their habitat requirements, may cause certain management techniques to affect species in the same system in different or even opposite ways (Morrison et al. 1996, Thirgood et al. 2000, Raimondi et al. 2015). For example, previous works have found potential conflicts between the conservation of some marsh passerines, such as Bearded Tits and other waterbirds, resulting from water management focused on individual species (Baldi 2005, Wilson and Peach 2005).

Potential conflicts derived from differences in habitat requirements can be identified between our study species. For instance, dry areas on the floodable surface had a positive effect on the abundance of Reed Bunting but a negative effect on the Bearded Tit. As previously said, the Great Reed Warbler is strongly related to reed formations (Martínez-Villalta et al. 2002, Méro et al. 2015), but some species were dependent on the development of other helophyte plants such as saw sedge and even avoided monospecific reed extensions. Management focused on creating heterogeneous wetlands could be the solution to these possible conservation conflicts derived from species-specific habitat requirements. In fact, the heterogeneity of these types of environments appears to be a relevant cause of the richness and abundance of marshland birds (Beemster et al 2010). This demonstrates the importance of conducting studies of this type to carry out integrated management actions and ultimately ensure that the conservation measures applied are as effective as possible (Poulin et al. 2002).

CONCLUSION

Marsh passerines have species-specific habitat requirements, which means that changes in the wetland system may affect them in different and even opposite ways. Because of the complexity of biological communities, integrative studies of communities are necessary to carry out appropriate management actions and avoid indirect effects of conservation measures focused on a single species.

Unsolved problems related to the wetland water regime in the Tablas de Daimiel National Park threaten its community of endangered birds. Reduction of aquifer overexploitation and restoration of the natural water regime should be considered a priority to guarantee the conservation of these species that, in spite of having specific habitat requirements, ultimately depend on the wetland hydrology. On the other hand, management focused on promoting habitat heterogeneity within the same wetland may be the best option to address species-specific differences in habitat selection processes and thus minimize potential conflicts.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/1953>

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Appendix 1. Table containing the coefficients obtained by the GLMMs.

Table A1.1. Best models obtained ($\Delta AIC < 2.0$) by automatic selection of GLMMs for each species. The values of Akaike Information Criterion (AIC), ΔAIC , weight (w) and the marginal (R_M^2) and conditional (R_C^2) r-squared values for each model are shown in the Coefficients column. Fixed effect column shows the presence ($\checkmark$) or absence (-) of the different habitat variables in the selected models, as well as the relative importance of the variable in the set of models (RIV) and a mean (Mean_E) and standard deviation (SD_E) of the Estimate values obtained for each variable. Finally, the variance explained, and standard deviation (SD) of the random effect variable (TFloodedArea) are shown in the last column.

Model	Coefficients					Fixed effects							Random effects	
	AIC	ΔAIC	w	R _M ²	R _C ²	Predictors	% <i>Cladium</i>	% <i>Phragmites</i>	% <i>Typha</i>	%DrierVeg	%OpenWater	%DrySurface	Variance	SD
Great Reed Warbler - <i>Acrocephalus arundinaceus</i>														
1	2021.1	0.0	0.16	0.036	0.342	-	✓	✓	✓	✓	✓	-	0.383	0.619
2	2021.4	0.3	0.14	0.019	0.353	✓	✓	✓	-	-	✓	-	0.425	0.652
3	2021.6	0.5	0.13	0.018	0.361	✓	-	-	✓	-	✓	-	0.443	0.666
4	2022.2	1.1	0.10	0.022	0.351	✓	✓	✓	-	✓	✓	-	0.417	0.646
5	2022.5	1.4	0.08	0.033	0.343	✓	-	-	✓	-	✓	✓	0.388	0.633
6	2022.6	1.5	0.08	0.035	0.339	✓	✓	✓	-	-	✓	✓	0.379	0.616
7	2022.8	1.7	0.07	0.013	0.371	✓	-	-	✓	-	-	-	0.468	0.684
8	2023.0	1.9	0.06	0.014	0.363	✓	-	-	-	-	✓	-	0.452	0.672
9	2023.1	2.0	0.06	0.019	0.356	✓	✓	✓	✓	-	✓	-	0.431	0.657
10	2023.1	2.0	0.06	0.038	0.341	✓	✓	✓	✓	✓	✓	-	0.379	0.616
11	2023.1	2.0	0.06	0.036	0.342	-	✓	✓	✓	✓	✓	✓	0.383	0.619
						Mean _E	-0.681	0.432	0.105	0.317	0.668	-0.177		
						SD _E	±0.478	±0.496	±0.469	±0.483	±0.510	±0.400		
						RIV	0.78	0.66	0.62	0.38	0.93	0.22		
Moustached Warbler - <i>Acrocephalus melanopogon</i>														
1	734.1	0.0	0.45	0.380	0.512	-	✓	✓	✓	✓	✓	✓	0.639	0.799
2	735.7	1.6	0.20	0.377	0.516	✓	✓	✓	-	✓	-	-	0.680	0.825
3	735.9	1.8	0.18	0.378	0.515	✓	✓	✓	-	✓	✓	-	0.668	0.817
4	736.0	1.9	0.17	0.380	0.514	✓	✓	✓	✓	✓	✓	✓	0.651	0.807
						Mean _E	1.091	-2.046	-0.885	-8.845	-1.399	-1.441		
						SD _E	±1.073	±1.017	±1.027	±1.166	±1.245	±1.667		
						RIV	0.55	1	0.62	1	0.8	0.62		
Reed Bunting - <i>Emberiza schoeniclus witherbyi</i>														
1	986.2	0.0	0.24	0.146	0.263	✓	-	✓	✓	-	✓	✓	0.287	0.536
2	986.8	0.6	0.18	0.148	0.274	✓	✓	✓	✓	✓	-	-	0.317	0.563
3	987.3	1.1	0.14	0.150	0.268	✓	✓	✓	-	-	✓	✓	0.292	0.540
4	987.6	1.4	0.12	0.149	0.268	✓	-	✓	✓	✓	✓	✓	0.294	0.542
5	987.6	1.4	0.12	0.149	0.268	✓	✓	✓	✓	-	✓	✓	0.294	0.542
6	988.0	1.8	0.10	0.148	0.266	✓	✓	✓	-	✓	✓	✓	0.293	0.541
7	988.1	1.9	0.10	0.147	0.266	✓	✓	✓	✓	✓	-	✓	0.292	0.540
						Mean _E	3.214	0.145	-1.348	-0.469	1.334	1.765		
						SD _E	±1.049	±1.056	±1.126	±0.997	±1.040	±1.154		
						RIV	1	0.64	0.76	0.5	0.72	0.82		
Savi's Warbler - <i>Locustella luscinioides</i>														
1	1819.7	0.0	0.45	0.270	0.342	✓	-	-	-	✓	✓	-	0.095	0.309
2	1821.1	1.4	0.22	0.268	0.339	✓	-	-	-	✓	✓	✓	0.092	0.304
3	1821.6	1.9	0.17	0.270	0.343	✓	-	✓	✓	✓	✓	-	0.097	0.311
4	1821.7	2.0	0.16	0.270	0.343	✓	✓	✓	✓	✓	✓	-	0.096	0.309
						Mean _E	1.311	0.004	-0.013	-2.757	0.775	0.087		
						SD _E	±0.013	±0.008	±0.026	±0.048	±0.040	±0.173		
						RIV	1	0.16	0.17	1	1	0.22		
Bearded Tit - <i>Panurus biarmicus</i>														
1	2355.2	0.0	0.45	0.418	0.606	-	-	-	-	✓	✓	✓	0.576	0.759
2	2356.9	1.7	0.19	0.419	0.604	-	-	-	✓	✓	✓	✓	0.566	0.752
3	2357.0	1.8	0.18	0.418	0.605	-	✓	-	-	✓	✓	✓	0.571	0.755
4	2357.0	1.8	0.18	0.420	0.606	✓	-	-	-	✓	✓	✓	0.569	0.755
						Mean _E	-0.059	-0.027	0.033	-5.713	0.907	-3.286		
						SD _E	±0.117	±0.055	±0.067	±0.048	±0.046	±0.050		
						RIV	0.18	0.18	0.19	1	1	1		