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Assessing variation in survival in *Acrocephalus* warblers: a comparative study of the life-history strategies of two closely related species

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The Spanish population of the vulnerable Moustached Warbler *Acrocephalus melanopogon*, which has undergone a continuous decline in recent decades, is the most important in Western Europe. It coexists with the widespread Reed Warbler *Acrocephalus scirpaceus*, whose population has increased. Differences in breeding productivity have been identified as a factor behind these diverging trends. We investigated these warblers' apparent adult survival rates to assess if this demographic parameter might also influence these different trends. Additionally, we tested to see whether there were any sex-related differences in survival and whether the different migration strategies of these two species (short-distance vs. long-distance migrant) might influence survival. To do so, we ringed both species intensively at 10 ringing stations located in El Marjal de Pego-Oliva Natural Park (Eastern Spain) in 2011–2015. In total, we ringed 502 Moustached Warblers and 459 Reed Warblers and built sex-known encounter histories for 396 (223 males and 173 females) and 394 (255 males and 139 females), respectively. We found that transient male Reed Warblers represented 35% of the population and that apparent survival rates did not differ between these two warblers, being 0.486 ± 0.050 (mean ± SE) for both male and female Moustached Warblers, 0.475 ± 0.105 for male and 0.471 ± 0.171 for female Reed Warblers. Our results indicate that there were no significant sex-related differences in survival in either species, as expected in species that exhibit bi-parental care behaviour. This study should encourage conservation managers and bird ringers alike to study survival as a means of improving knowledge of avian population dynamics.

Key words: bird conservation, capture-recapture models, migration, Moustached Warbler, Reed Warbler, ringing, winter survival.

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Survival is a critical parameter for assessing the viability of bird populations (Garcias & Tavecchia 2018, Schwartz *et al.* 2021) and is affected by a number of different factors. Climatic conditions can significantly restrict the seasonal availability of food resources and so will influence survival and other demographic parameters (Robinson *et al.* 2007). Specifically, extreme temperatures have a direct impact on survival rates, influencing not only the immediate well-being of individuals but also long-term population viability (Gardner *et al.* 2022). Additionally, various factors related to species' life history – above all the demographic costs associated with reproduction – can lead to differences in survival rates (Scholer *et al.* 2020), which may vary between sexes (Sanz-Aguilar *et al.* 2017). During their annual cycle, migrations are among the most physically demanding feats that some birds perform (Buechley *et al.* 2021), as they have to face up to sustained energy expenditure over long periods, cope with environmental challenges, and make physiological adaptations when preparing for their journeys (Lennox *et al.* 2016). Thus, adverse non-breeding conditions can significantly impact songbird survival rates during both migration and breeding periods (Cooper *et al.* 2024).

To increase their chances of survival, some species exhibit migratory behaviour primarily when abandoning their breeding grounds due to a predictable period of resource scarcity, unsuitable climatic conditions and/or high predation risk (Pelletier *et al.* 2020). This strategy not only increases annual survival rates but also boosts the likelihood of successful subsequent breeding seasons. The time-allocation hypothesis (Greenberg 1980), which aims to explain variation in survival and reproduction in temperate-breeding bird species with differing migratory strategies, suggests that long-distance migratory species invest less time in breeding than short-distance migrants but compensate for their subsequent lower fecundity by investing more time and energy in migrating to areas with abundant resources, thereby enhancing winter survival rates. Thus, species that migrate long distances in search of more favourable locations in which to spend the non-breeding season should have higher survival rates than short-distance migrants despite the enormous risks that migration entails (Winger & Pegan 2021).

Survival may also differ significantly between sexes (Monticelli *et al.* 2014). Although a higher survival rate in males than in females is observed in numerous populations, the deviation from parity is not usually statistically significant (Payevsky 2021). A significant component of male mortality is linked to defending and securing territories, whereas increased reproductive output and time spent in the nest may lead to higher female mortality (Liker & Székely 2005, Székely *et al.* 2014). Some bird species have a bi-parental care system wherein both males and females incubate and help provision the chicks (Wojczulanis-Jakubas *et al.* 2023). This cooperative behaviour is particularly evident in species such as the Moustached Warbler *Acrocephalus melanopogon* and the Reed Warbler *Acrocephalus scirpaceus*, in which both parents are actively involved in raising their offspring and do so at comparable rates. This cooperation between the sexes in parental care is expected to have an equal effect on the survival of both species.

Here, we assess the influence of migration strategies on survival in a resident/short-distance migrant (Moustached Warbler) and a long-distance migrant (Reed Warbler) and hypothesise (1) that the survival of long-distance migrants should be greater than that of the resident/short-distance migrants; and (2) that, due to their bi-parental care behaviour, there will be no differences between these two species in their sex-related apparent survival rates.

Material and methods

Species studied

The population of Moustached Warblers in Western Europe is mainly concentrated along the Mediterranean coast of Spain and France (López Iborra & Castany 2022). In Spain, breeding Moustached Warblers are resident or migrate over short distances and begin to lay in late March/early April (Ceresa *et al.* 2016a). Their distribution is notably fragmented, with the largest numbers found in the S'Albufera de Mallorca and in the wetlands of the Valencia Region, primarily in El Marjal de Pego-Oliva Natural Park and Marjal de Xeresa (Castany & López 2006). Recent surveys have highlighted a substantial decline in this species over much of its range in Spain (López Iborra & Castany 2022). Furthermore, Lucio-Puig *et al.* (2024) found a negative trend in Moustached Warbler productivity related to geographical and site-specific factors, and to the negative effect of rising temperatures and intense precipitation events during nesting and rearing seasons. The effects of these factors also suggest the existence of mismatches between breeding phenology and food availability (McKinnon *et al.* 2012). By contrast, the Reed Warbler is widely distributed across Europe and its populations increased considerably in Spain in 2011–2021 (Carrascal *et al.* 2023). Moreover, this species may in fact benefit from rising temperatures that could help extend its breeding season (Halupka *et al.* 2008) and, therefore, increase its productivity as a response to global warming (Lucio-Puig *et al.* 2024). Reed Warblers overwinter in sub-Saharan Africa and start laying in Western Europe in May (Kennerley & Pearson 2010).

Study area and data collection

The research took place in El Marjal de Pego-Oliva Natural Park (Eastern Spain, 38°52'N 0°04'W). Spanning 1,250 ha, this park boasts extensive reedbeds occupied predominantly by Common Reed *Phragmites australis* and Narrowleaf Cattail *Typha angustifolia*, and a series of water bodies and paddy fields (Fig. 1). Between 2011 and 2015, we conducted intensive sampling from late February to July at 10 ringing stations and captured birds on an almost daily basis at one randomly selected station each day, using six 10-m mist nets (16 mm mesh). Bird ringing started 30 min before dawn and lasted for four hours. Captured birds were ringed, sexed and aged whenever possible following Svensson (1996) before release.

Survival analysis

The apparent survival probability (Φ_i) is the likelihood that an individual in the population at time i is still alive and in the population at time $i+1$ (Schmidt *et al.* 2007). To estimate the apparent survival of our two sympatric target species, we only considered birds ringed and recaptured during the three months of each breeding season. According to Ceresa *et al.* (2020), breeding seasons last from April to June for the Moustached Warbler and from May to July for the Reed Warbler. Following Lebreton *et al.* (1992), we designed a capture-mark-recapture approach for these breeding seasons. We only analysed adult breeding birds (i.e. those born before the year of capture) whose sex was known to test for differences in survival between sexes and species. Juvenile birds are less philopatric than adult birds (Mátrai *et al.* 2012, Ceresa *et al.* 2016b), which can make it difficult to distinguish between juvenile dispersal and mortality during the early life stages (Sharp *et al.* 2008).

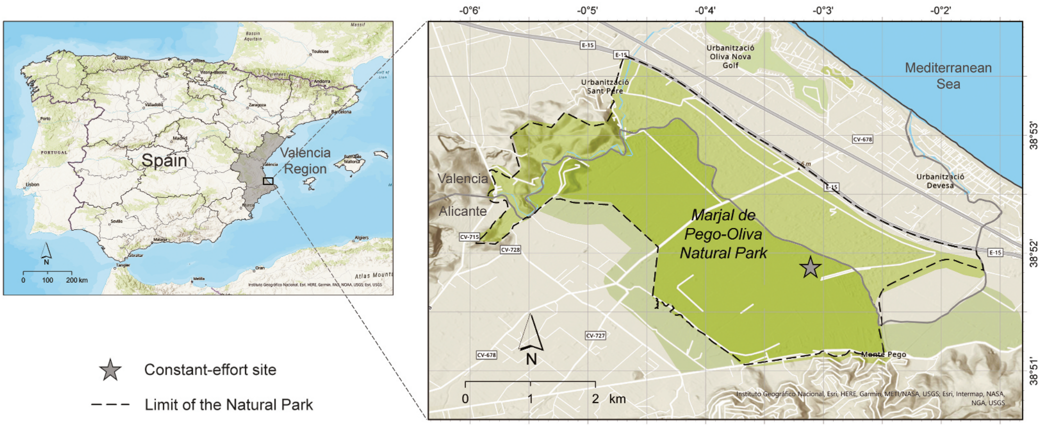

Figure 1. Left: location of El Marjal de Pego-Oliva Natural Park in the provinces of Valencia and Alicante (Valencia Region, Eastern Spain). Right: approximate location of the ringing area containing the 10 ringing stations in the Natural Park.
Localització del Parc Natural de la Marjal de Pego-Oliva, entre les províncies de València i Alacant (València, Est d'Espanya) (esquerra) i ubicació aproximada de l'àrea d'anellament que conté les deu estacions d'anellament dins dels límits del Parc Natural (dreta).

Thus, we only used capture-recapture histories of adult birds that were trapped at least once during the study period to estimate the apparent annual survival in 2011–2015. Survival analyses were run in the program *MARK v9* (White & Burnham 1999). Firstly, we performed a goodness of fit (GOF) test using the program *U-CARE* (Choquet *et al.* 2009) to investigate the validity of the data for our global extended model $\Phi(\sim$ sex x time$)$ $p(\sim$ sex x time$)$ in accordance with the assumptions of the Cormack-Jolly-Seber model (hereafter, CJS model). Various tests from the program *U-CARE* were conducted, including 3SR, 2CT and 2CL. The 3SR test is one of the components of the GOF and is relevant for detecting differences in the probability that 'newly marked' and 'already marked' individuals first encountered at occasion *i* will be recaptured. For instance, the 3SR test is significant when there is an age effect on survival, if the marking causes disturbance, or due to the presence of transients (Lebreton *et al.* 1992, Belda *et al.* 2007). The 3SM test checks for homogeneity, that is, whether there is any difference in the expected time of first reencounter for 'newly marked' and 'already marked' individuals encountered at occasion *i* and seen again at least once. The 2CT test explores whether there is a difference in the probability of being recaptured at time $i+1$ for birds encountered and not encountered on occasion *i* (conditional on their presence on both occasions). The 2CT test is significant if there is either an immediate trap effect on the recapture probability or if non-random temporal emigration occurs. Finally, the 2CL test explores whether there is any difference in the expected time of the next recapture for birds encountered and not encountered at occasion *i* (conditional on their presence on both occasions *i* and $i+2$) (Choquet *et al.* 2020).

For male Reed Warblers, we used a time-since-marking (TSM) approach as a global model as it is the most parsimonious when the 3SR test yields significant results (Pradel *et al.* 1997). The significance of this test could be explained by the presence of transient individuals, i.e. birds that after being marked and released permanently emigrate from the sampling site and so are no longer available for future encounters. This model allows for the survival probability for period *i* to differ between groups of individuals (residents and transients). Thus, if there are transients in the population, the apparent survival of birds captured for the first time – which might include both residents and transients – will differ from resident individuals (those captured previously). Therefore, the following TSM model was used as the global model: $\Phi(\sim$time/time$)$ $p(\sim$time$)$. To estimate the percentage of resident and transient male Reed Warblers, we divided the estimated survival over the initial survival – where both residents and transients are present in a sample – by the estimated survival over the same interval when only residents are present in the sample (Pradel *et al.* 1997). As well, we built an additive model – $\Phi(\sim$time+time$)$ $p(\sim$time$)$ – to force transients and residents to have the same difference in survival rates every year. Parametric bootstrap methods were used to estimate the amount of overdispersion, known as the variance inflation factor ($\hat{c}$), for both species. Model selection was based on the Akaike Information Criterion AIC (Burnham & Anderson 2004), which was corrected accordingly when $\hat{c}$ values indicated overdispersion ($\hat{c} > 1.0$) and gave the quasi-likelihood Akaike's Information Criterion corrected for sample size (QAICc). Following Lebreton *et al.* (1992), we selected the most parsimonious structural model with the largest QAICc weight. Finally, we used the software *Contrast* (Hines & Sauer 1989) to statistically compare estimates of survival between sexes and species (Moustached Warbler vs. Reed Warbler).

Results

We were able to construct individual encounter histories for 396 (223 males and 173 females) Moustached Warblers and for 394 (255 males and 139 females) Reed Warblers of known sex, out of a total 502 Moustached Warblers and 459 Reed Warblers ringed. Details of the number of individuals captured and released per sex on each occasion (interval years), followed by year and total recaptures during the study period, are provided (Table 1).

The overall goodness of fit (GOF) from the global extended model including sex and time – $\Phi(\sim$ time x sex$)$ $p(\sim$ time x sex$)$ – was not significant for either Moustached Warblers ($\chi^2_{14} = 16.326$, $P = 0.294$) or Reed Warblers ($\chi^2_{10} = 14.458$, $P = 0.153$). However, the 3SR test

Table 1. Contingency table of the number of captures per sex and occasion (yearly intervals) for Moustached and Reed Warblers in 2011–2015. *Ri* is the number of birds released at occasion *i* (new adults ringed and recaptured previously ringed adults); *ri* is the total number of recaptures of the *Ri* birds originally released at occasion *i*. The columns with the years indicate the recaptures of birds released on each occasion.
Taula de contingència del nombre de captures per sexe i ocasió (interval d'anys) de la boscarla mostatxuda i la boscarla de canyar durant el període 2011-2015. Ri és el nombre d'ocells alliberats en la ocasió i (nous adults anellats i adults recapturats que havien sigut anellats prèviament) i ri són les recaptures totals entre els Ri alliberats originalment en l'ocasió i. Les columnes amb els anys fan referència a les recaptures dels ocells alliberats en cada ocasió.

Occasion *i*	***Ri***	**2012**	**2013**	**2014**	**2015**	***ri***
Male Moustached Warbler						
1 (2011-2012)	71	13	4	1	0	18
2 (2012-2013)	60	0	5	6	2	13
3 (2013-2014)	38	0	0	16	0	16
4 (2014-2015)	74	0	0	0	17	17
Female Moustached Warbler						
1 (2011-2012)	49	11	2	2	1	16
2 (2012-2013)	40	0	8	4	0	12
3 (2013-2014)	35	0	0	7	0	7
4 (2014-2015)	59	0	0	0	7	7
Male Reed Warbler						
1 (2011-2012)	42	5	2	0	0	7
2 (2012-2013)	69	0	7	4	2	13
3 (2013-2014)	67	0	0	6	1	7
4 (2014-2015)	61	0	0	0	8	8
Female Reed Warbler						
1 (2011-2012)	29	4	1	0	0	5
2 (2012-2013)	39	0	1	2	1	4
3 (2013-2014)	27	0	0	0	0	0
4 (2014-2015)	34	0	0	0	5	5

indicated the presence of transients amongst the male Reed Warblers ($\chi^2_3 = 10.286$, $P = 0.016$) (Table 2), suggesting that more birds than expected under the CJS model were seen only once, i.e. transient individuals were present in the marked population. Consequently, we built a new global model including transients for male Reed Warblers: $\Phi(\sim\text{time/time})\ p(\sim\text{time})$. The GOF for this model was approximately equivalent to the overall GOF for the CJS model without the 3SR component (Belda *et al.* 2007, Choquet *et al.* 2009) and so meets the CJS model assumptions. For female Reed Warblers, the 3SR test provided no evidence of transients ($\chi^2_2 = 0.826$, $P = 0.661$), so the new global model was time-dependent $\Phi(\sim\text{time})\ p(\sim\text{time})$.

Some evidence of overdispersion was detected for Moustached Warblers ($\hat{c} = 1.166$) and for both male ($\hat{c} = 1.195$) and female ($\hat{c} = 1.236$) Reed Warblers, and so results were corrected accordingly. For Moustached Warblers, the model that best fitted the data was constant apparent survival and a time-dependent probability of recapture: $\Phi(.)\ p(\sim\text{time})$ (model weight [w_i] = 0.430) (Table 3). This model had the greatest weight and was over twice as well supported as the next best model, which included sex. Thus, the best model provided a constant survival of 0.486 ± 0.050 (mean ± SE) (95% CI: 0.391 - 0.583) and a variable prob-

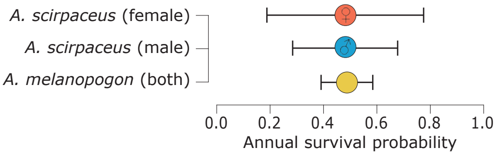

Figure 2. Average apparent annual survival probabilities and confidence intervals for Moustached and Reed Warblers in El Marjal de Pego-Oliva Natural Park in 2011–2015.
Probabilitat de supervivència aparent anual mitjana i intervals de confiança de la boscarla mostatxuda i boscarla de canyar al Parc Natural de la Marjal de Pego-Oliva durant el període 2011–2015.

Table 2. Overall GOF and specific tests for the starting global model Φ(~ sex x time) p(~ sex x time). Note the adequacy of the data for Moustached Warblers and the lack of fit in test 3SR for male Reed Warblers. Therefore, a TSM (time-since-marking) model was used as the new starting model for male Reed Warblers.
Test de bondat global i específics del model inicial Φ(~ sexe x temps) p(~ sexe x temps). Cal notar l'adequació de les dades de la boscarla mostatxuda i la manca d'ajustament en test 3SR en els mascles de la boscarla de canyar. Per tant, es va establir un model TSM (de temps des del marcatge) com a nou model inicial per als mascles de boscarla de canyar.

	Moustached Warbler				**Reed Warbler**			
	Male		**Female**		**Male**		**Female**	
	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Test 3SR	5.415	0.143	4.007	0.261	10.286	0.016	0.826	0.661
Test 3SM	0.331	0.565	0.000	1	0.000	1	0.000	1
Test 2CT	4.910	0.086	1.036	0.596	0.826	0.066	0.708	0.400
Test 2CL	0.000	1	0.630	0.429	0.000	1	0.000	1
Overall test	χ^2 = 16.326 df = 14 P = 0.294				χ^2 = 11.113 df = 5 P = 0.050		χ^2 = 1.534 df = 4 P = 0.820	

ability of recapture between years with a maximum of 0.630 ± 0.012 (95% CI: 0.371 - 0.831) and a minimum of 0.288 ± 0.071 (95% CI: 0.170-0.444). The most parsimonious reduced model including sex – Φ (~sex) p(~time) (model weight [w_i] = 0.166) – provided a constant survival value of 0.496 ± 0.055, (95% CI: 0.389 - 0.602) for males and 0.469 ± 0.064, (95% CI: 0.348 - 0.594) for females (Figure 2). These results did not support differing survival rates for the two sexes according to the overlap between CI and the results of the *Contrast* test (χ^2 = 0.102, df = 1, P = 0.749).

For male Reed Warblers, the best-supported model was Φ(.) p(.) (w_i = 0.373, Table 4), with an estimated apparent survival of 0.475 ± 0.105 (95% CI: 0.283 - 0.673) (Figure 2) and a constant probability of recapture of 0.229 ± 0.078 (95% CI: 0.110 - 0.417). The second-best model had only half the support and was a TSM model, with constant survival and probability of recapture: Φ(./.) p (.) (w_i = 0.190). This model provided an estimated apparent survival of 0.343 ± 0.136 (95% CI: 0.138 - 0.631) for the first group, which included residents and transients, and an estimated apparent survival of 0.527 ± 0.123 (95% CI: 0.297 - 0.746) for resident birds. These results enabled us to estimate the proportion of residents at 65% and transients at 35%. The third-best model was the additive model Φ(~time + time) p(.), where the residents are modelled as a linear function of transients plus an additive constant.

For female Reed Warblers, the model that best fitted the data was Φ(.) p(.) (w_i = 0.64, Table 5), which was over four times better supported than the second-best model. The model estimated an apparent survival of 0.471 ± 0.171 (95% CI: 0.187 - 0.774) (Figure 2) and a probability of recapture of 0.166 ± 0.096 (95% CI: 0.048 -

Table 3. Model selection for adult Moustached Warbler survival in 2011–2015 in El Marjal de Pego-Oliva Natural Park, Eastern Spain. Shown are the five top subsets of models nested within the starting global model Φ(~ sex x time) p(~ sex x time). QAICc = Quasi-Akaike Information Criteria scores; ΔQAICc = difference of models' QAICc values in relation to the top model; QAICc (w) = Quasi-Akaike weights; No.Par = Number of parameters; QDeviance = deviance of the model.
Selecció de models de supervivència d'adults de boscarla mostatxuda durant 2011-2015 al Parc Natural de la Marjal de Pego-Oliva, Est d'Espanya. Cinc millors models niats dins del model global Φ(~ sexe x temps) *p(~* sexe x temps). *QAICc = valors del Quasi-Akaike criteri d'informació; ΔQAICc = diferència dels valors de QAICc respecte al millor model; QAICc (w) = pesos Quasi-Akaike; No.Par = Nombre de paràmetres; QDeviance = desviació del model.*

Model	QAICc	ΔQAICc	QAICc (w)	No.Par	QDeviance
Φ(.) p(~ time)	510.30	0.00	0.51	5	44.73
Φ(sex) p(~ time)	512.20	1.90	0.20	6	44.56
Φ(.) p(~ sex x time)	513.64	3.34	0.09	9	39.77
Φ(~ time) p(~ time)	513.99	3.69	0.08	7	44.29
Φ(~ sex) p(~ sex x time)	514.56	4.26	0.06	10	38.60

Table 4. The five top models used to test adult male Reed Warbler survival in 2011–2015 in El Marjal de Pego-Oliva Natural Park, Eastern Spain. QAICc = Quasi-Akaike Information Criteria scores; ∆QAICc = difference of models' QAICc values in relation to the top model; QAICc (w) = Quasi-Akaike weights; No.Par = Number of parameters; QDeviance = deviance of the model. The slash / indicates a TSM model, i.e. the apparent survival of two classes (residents and transients), while + indicates the additive model with a common intercept for both classes.
Cinc millors models per testar la supervivència de mascles adults de boscarla de canyar durant 2011-2015 al Parc Natural de la Marjal de Pego-Oliva, Est d'Espanya.. QAICc = valors del Quasi-Akaike criteri d'informació; ∆QAICc = diferència dels valors de QAICc respecte al millor model; QAICc (w) = pesos Quasi-Akaike; No.Par = Nombre de paràmetres; QDeviance = desviació del model. La barra inclinada / indica un model TSM, és a dir la supervivència aparent de dos grups (residents i transitoris), i + indica el model additiu amb una intercepció comuna per a les dues classes.

Model	Q AICc	∆QAICc	QAICc (w)	No.Par	QDeviance
$\Phi(.)\ p(.)$	206.37	0.00	0.37	2	16.92
$\Phi(./.)\ p(.)$	207.71	1.34	0.19	3	16.21
$\Phi(\sim \text{time} + \text{time})\ p(.)$	207.73	1.36	0.18	5	12.08
$\Phi(./\text{time})\ p(.)$	209.48	3.10	0.07	5	13.82
$\Phi(\sim \text{time}/.)\ p(.)$	211.74	5.36	0.02	6	13.98

0.437). The second-best model – $\Phi(\sim\text{time})\ p(.)$ $(w_i = 0.14)$ – was > 2 ∆QAICc. These results did not support any different survival rate between sexes due to the overlap between CI and the results obtained in *Contrast* ($\chi^2 = 0.000$, $df = 1$, $P = 0.983$).

When comparing the survival rates between Moustached and Reed Warblers, we found no significant differences ($\chi^2 = 0.014$, $df = 2$, $P = 0.993$).

Discussion

We found no significant differences in the survival rates of the resident/short-distance migrant Moustached Warbler or the long-distance migrant Reed Warbler. This suggests that the benefit of increased resource availability during winter for the Reed Warbler is balanced out by the costs associated with the migratory process (e.g. energetic costs and mortality risk) (Alerstam *et al.* 2003). Moreover, we found no differences in apparent survival between sexes for either Moustached or Reed Warblers, which agrees with previous research (Castany 2003, López-Iborra *et al.* 2006, Thaxter *et al.* 2006). This was expected since males and females in both species contribute similarly during incubation and the parental care of the chicks (Cramp 1992).

Estimates of apparent survival of Moustached Warblers in El Prat de Cabanes-Torreblanca Natural Park, Castellón, Spain, (Castany 2003) were higher in 1990–1993, with values of 0.773 ± 0.044 (95% CI: 0.676 - 0.847). The factors behind this elevated survival could be explained by local and/or temporal conditions given that these estimates decreased in 1994–2002 and eventually fell to similar values to those found in our study, i.e. 0.522 ± 0.038 (95% CI: 0.448

Table 5. Selection of a reference model for adult female Reed Warbler survival in 2011–2015 in El Marjal de Pego-Oliva Natural Park, Eastern Spain. Shown are the four top subsets of models nested within the starting global model $\Phi(\sim \text{time})\ p(\sim \text{time})$. QAICc = Quasi-Akaike Information Criteria scores; ∆QAICc = difference of models' QAICc values in relation to the top model; QAICc (w) = Quasi-Akaike weights; No.Par = Number of parameters; QDeviance = deviance of the model.
Selecció del model de referència per testar la supervivència de femelles adultes de boscarla de canyar durant 2011-2015 al Parc Natural de la Marjal de Pego-Oliva, Est d'Espanya. Quatre millors models niats en el model global $\Phi(\sim \text{temps})\ p(\sim \text{temps})$. QAICc = valors del Quasi-Akaike criteri d'informació; ∆QAICc = diferència dels valors de QAICc respecte al millor model; QAICc (w) = pesos Quasi-Akaike; No.Par = Nombre de paràmetres; QDeviance = desviació del model.

Model	QAICc	∆QAICc	QAICc (w)	No.Par	QDeviance
$\Phi(.)\ p(.)$	90.76	0.00	0.64	2	13.07
$\Phi(\sim \text{time})\ p(.)$	93.75	2.98	0.14	5	9.66
$\Phi(.)\ p(\sim \text{time})$	93.78	3.01	0.14	5	9.69
$\Phi(\sim \text{time})\ p(\sim \text{time})$	95.12	4.36	0.07	7	6.60

- 0.596). The survival rates found during the first period (1990–1993) are higher than those found in many passerines species, while our estimates and the estimates from El Prat de Cabanes-Torreblanca from 1994–2002 are close to the expected values for many passerines (Siriwardena *et al.* 1998).

The survival estimates for the Reed Warbler were very similar to those estimated for other Mediterranean Spanish wetlands. López-Iborra *et al.* (2006) estimated an apparent survival of 0.445 ± 0.018 (95 CI: 0.410 - 0.480) in El Hondo Natural Park (Alicante, Spain) and a value of 0.471 ± 0.054 (95 CI: 0.369 - 0.576) for the mouth of the river Mijares. Such similar results from different wetlands and time periods suggest that the regional conditions driving survival in breeding sites are far less significant than the mortality that occurs during migration and in winter in sub-Saharan Africa (Wierucka *et al.* 2016).

The rejection of the 3SR test for male Reed Warblers indicates either the presence of transients, an age effect or a marking effect. However, it is likely that the presence of transients is the most plausible explanation as Reed Warblers are known to have a great capability to disperse over large distances (Ceresa *et al.* 2016b). Many of the males trapped were probably on migration or dispersing and still had cloacal protuberances. The TSM model indicates a lower local survival probability for transients than residents, which could be due to a negative effect provoked by marking or disturbance (Oro & Doak 2020); nevertheless, this seems unlikely as this effect should have also been detected in female Reed and Moustached Warblers.

Our study provides new insights into the vital rates of adult birds of two sympatric *Acrocephalus* warblers. However, future research into the effect on juvenile survival might provide different results for these two species as fledging age and body reserves accumulated during parental care are probably an important factor driving survival in the first stages of life (Maness & Anderson 2013). Surveys in some of the most important breeding areas in Western Europe indicate an important decline in Moustached Warbler populations (Keller *et al.* 2020, López Iborra & Castany 2022), which, based on our partial results in El Marjal de Pego-Oliva Natural Park, may be connected to productivity rather than to survival (Lucio-Puig *et al.* 2024) and to a potential mismatch between breeding phenology and food availability. These results should encourage more monitoring efforts to be made for these species as a means of improving knowledge of their population dynamics.

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Resum

Estima de la variació de la supervivència en dues espècies d'*Acrocephalus*: un estudi comparatiu amb espècies estretament emparentades

La població espanyola de la vulnerable boscarla mostatxuda *Acrocephalus melanopogon*, que ha experimentat un continu declivi en les últimes dècades, és la més important d'Europa occidental. Aquesta espècie coexisteix amb l'àmpliament distribuïda boscarla de canyar *Acrocephalus scirpaceus*, la població de la qual ha augmentat. Les diferències en la productivitat durant l'època de cria s'han identificat com un factor darrere d'aquestes tendències divergents. Vam investigar les taxes aparents de supervivència d'adults d'aquestes dues espècies per avaluar si aquest paràmetre demogràfic també podria influir en aquestes diferents tendències. A més, vam testar si hi havia diferències relacionades amb el sexe en la supervivència i si les diferents estratègies de migració d'aquestes dues espècies (migrants de curta i de llarga distància) podrien influir en la supervivència. Per això, vam anellar ambdues espècies de manera intensiva en 10 estacions d'anellament situades al Parc Natural del Marjal de Pego-Oliva (est d'Espanya) durant el període 2011–2015. En total, anellàrem 502 boscarles mostatxudes i 459 boscarles de canyar, que van permetre construir un historial de recaptures per a 396 (223 mascles i 173 femelles) i 394 (255 mascles i 139 femelles), respectivament. Vam trobar que els mascles transeünts de boscarla de canyar representaven el 35% de la població i que les taxes de supervivència aparents no variaven entre aquestes dues espècies, sent de 0,486 ± 0,050 (mitjana ± SE) tant per als mascles com per a les femelles de boscarla mostatxuda, i de 0,475 ± 0,105 per als mascles i 0,471 ± 0,171 per a les femelles de boscarla de canyar. Els nostres resultats indiquen que no hi va haver diferències significatives relacionades amb el sexe en la supervivència en cap d'aquestes dues espècies, com s'esperava en les que presenten un comportament de cura biparental. Aquest estudi hauria d'encoratjar els gestors de la conservació i els anelladors a estudiar la supervivència com a mitjà per millorar el coneixement de la dinàmica poblacional dels ocells.

Resumen

Estima de la variación de la supervivencia en dos especies de *Acrocephalus*: un estudio comparativo con especies estrechamente emparentadas

La población española del vulnerable carricerín real *Acrocephalus melanopogon*, que ha experimentado un continuo declive en las últimas décadas, es la más importante de Europa occidental. Esta especie coexiste con el ampliamente distribuido carricero común *Acrocephalus scirpaceus*, cuya población ha aumentado. Las diferencias en la productividad durante la época de cría se han identificado como un factor detrás de estas tendencias divergentes. Investigamos las tasas aparentes de supervivencia de adultos de estas dos especies para evaluar si ese parámetro demográfico también podría influir en estas distintas tendencias. Además, testamos si existían diferencias relacionadas con el sexo en la supervivencia y si las diferentes estrategias de migración de estas dos especies (migrantes de corta y larga distancia) podrían influir en la supervivencia. Por eso, anillamos ambas especies de forma intensiva en 10 estaciones de anillamiento situadas en el Parque Natural del Marjal de Pego-Oliva (este de España) durante el período 2011–2015. En total, anillamos 502 carricerines reales y 459 carriceros comunes, que permitieron construir un historial de recapturas para 396 (223 machos y 173 hembras) y 394 (255 machos y 139 hembras), respectivamente. Encontramos que los machos transeúntes de carricero común representaban el 35% de la población y que las tasas de supervivencia aparentes no variaban entre estas dos especies, siendo de 0,486 ± 0,050 (media ± SE) tanto para los machos como para las hembras de carricerín real, y de 0,475 ± 0,105 para los machos y 0,471 ± 0,171 para las hembras de carricero común. Nuestros resultados indican que no hubo diferencias significativas relacionadas con el sexo en la supervivencia en ninguna de estas dos especies, como se esperaba en aquellas que presentan un comportamiento de cuidado biparental. Este estudio debería alentar a los gestores de la conservación y a los anilladores a estudiar la supervivencia como medio para mejorar el conocimiento de la dinámica poblacional de las aves.

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