

Stopover by reed-associated warblers *Acrocephalus* spp. in wetlands in the southeast of the Bay of Biscay during autumn and spring passage

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Understanding how migratory *Acrocephalus* warblers use the wetlands along the coast of the southeast of the Bay of Biscay during autumn and spring migrations is vital from both conservation and management perspectives. Our aim was to explore whether *Acrocephalus* warblers use the region in spring in the same way as in autumn. We used ringing data obtained from three wetlands (Adour, Txingudi and Urdaibai) during the autumn of 2011 and the spring of 2012. Overall, the migration in spring was much weaker than in autumn. The remarkable scarcity of Reed Warblers (*A. scirpaceus*) in spring may be due in part to the fact that they tend to pass through even later than Sedge (*A. schoenobaenus*) and Aquatic (*A. paludicola*) Warblers, although, judging from additional data, the spring passage of the Reed Warbler is still lower than in autumn. Sedge Warblers in spring apparently had shorter staying periods than in autumn, but had similar fuel loads.

Key words: warblers, *Acrocephalus*, coastal marshes, reed beds, migration, Bay of Biscay

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Each autumn, millions of birds that have bred in northern Europe migrate to their wintering areas in southern Europe, northern Africa and sub-Saharan Africa (Biebach 1990). The return route is taken in spring. The European Atlantic coast, including the Bay of Biscay, channels one of the chief migratory flows between Europe and Africa (Newton 2008).

The wetlands situated along the coast of the Bay of Biscay in southwest Europe host huge numbers of migrant birds *en route* to Africa during the autumn migration period (Caillat *et al.* 2005, González *et al.* 2007, Mendiburu *et al.* 2009, Chenaival *et al.* 2011). Some, especially trans-Saharan birds (i.e. those overwintering

south of the Sahara desert), use these wetlands to build up their fuel reserves to be able to reach Africa without further refuelling stops (Arizaga *et al.* 2011). These sites thus play a vital role as target fuelling stopovers in autumn. By contrast, previous studies indicate a much weaker flow of migrants in spring along the southeastern shores of the Bay of Biscay (Arizaga *et al.* 2010c), thus suggesting only a possible marginal importance – in terms of the number of migrants that decide to land – for this area as a stopover site during this period. The term ‘stopover’ is here used to refer to a site where migrants decide to land just to rest or to refuel, or both. However, these previous studies were conducted with a relatively small

sampling effort and only at one site (Txingudi), which may not be representative of the south-eastern Bay of Biscay (Arizaga & Barba 2009b). Therefore, it remains to be seen whether or not the wetlands in this area are also widely used as stopover sites during the spring migration period.

A paradigmatic group of the trans-Saharan birds that use these marshlands in large numbers are the *Acrocephalus* warblers (Mendiburu *et al.* 2009, Fontanilles *et al.* 2010), some of which are threatened by extinction (in particular, the Aquatic Warbler *A. paludicola*; Julliard *et al.* 2006). Understanding how these *Acrocephalus* warblers use the wetlands along this coast as stopover sites in different periods of the year (autumn and spring migrations) is important from both conservation and management points of view.

A first approach when assessing whether a zone is used as a stopover site by migrants is to determine how many birds occur at that site. In spring, less intensive use of the wetlands in the region is to be expected in light of two factors: (i) migration in spring is faster than in autumn since spring days are longer and migrants have more time to gain fuel, thereby permitting shorter stopover periods (Newton 2008); and (ii) some species such as Reed Warbler (*A. scirpaceus*; Cantos 1998) and Aquatic Warbler (Atienza *et al.* 2001) have been reported to return from Africa to their breeding areas across more easterly routes.

The proportion of recaptures within a season can be used as a simple approach to estimate the use (permanence) of migrants at a site (Ellegren 1991, Lavee *et al.* 1991, Grandío 1997, Arizaga *et al.* 2010a). The underlying assumption is that if the proportion of recaptures in a species at a site differs between seasons without any variation in the sampling effort, it is because that species has shorter staying periods, which translates as a lower proportion of recaptures. Additionally, the probability of recapture must also be kept constant between periods and within sites (Schaub *et al.* 2001). If migrants travel faster in spring because they have shorter stopover periods (Newton 2008), we would expect a greater proportion of recaptures (i.e. a higher proportion of migrants stopping over for more than one day) in autumn than in spring.

The amount of fuel that migrants gain at a stopover site can also be used to analyze and assess the relative importance of an area within

a migration-strategic context (Schaub & Jenni 2000, Dierschke & Delingat 2001, Arizaga *et al.* 2011). Thus, some *Acrocephalus* warblers, above all Sedge Warblers (*A. schoenobaenus*), seem to gain all the fuel they need to reach at least the northern Sahara in central-western Europe along the Atlantic coast of France and northern Iberia (Bibby & Green 1981, Grandío 1998). High fuel loads at given localities mean that migrants will depend on other stopover sites to acquire the fuel they need to reach successfully their destination areas.

The aim of this work was to explore whether marsh-related *Acrocephalus* warblers use the coastal marshes in the southeast Bay of Biscay as stopover sites in spring in the same way as in autumn (particularly in terms of abundance, stopover duration and fuel load). We used ringing data to assess the number of captures, the proportion of recaptures and fuel load in *Acrocephalus* warblers to test this hypothesis.

Material and methods

Study area

This study was carried out in the three main wetlands in the southeast of the Bay of Bis-

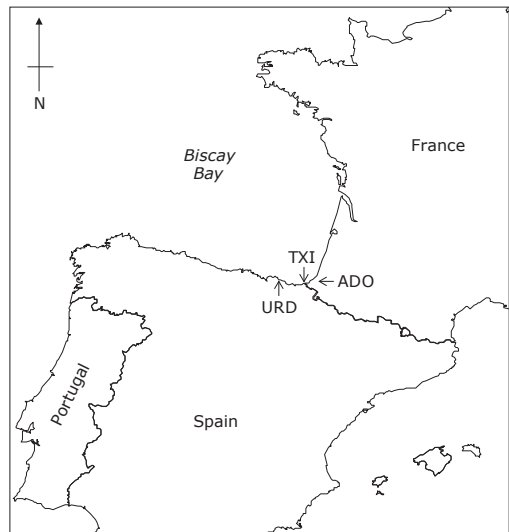


Figure 1. Location of the sampling sites. ADO: Adour; TXI: Txingudi; URD: Urdaibai.

Localització dels llocs de mostreig on s'ha dut a terme l'estudi. ADO: Adour; TXI: Txingudi; URD: Urdaibai.

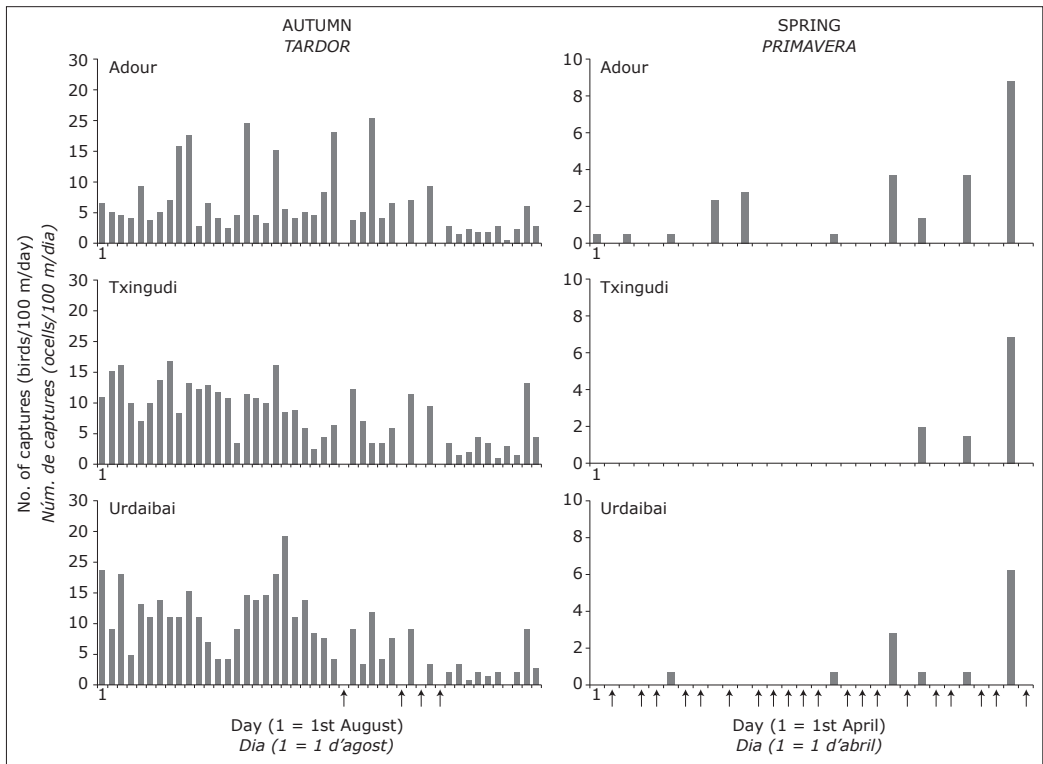


Figure 2. Timing of captures of *Acrocephalus* warblers at the three wetland study sites in the southeast of the Bay of Biscay during autumn and spring migration. Arrows indicate non-sampling days, which were frequent in spring due to rain.

Fenologia de les captures de boscarles del gènere Acrocephalus a tres aiguamolls del sud-est del golf de Biscaia durant la migració de tardor i primavera. Les fletxes indiquen els dies sense mostreig (principalment a la primavera i a causa de les pluges).

cay: Urdaibai (43°20'N, 02°40'W), Txingudi (43°21'N, 01°49'W) and Adour (43°27'N, 01°28'W) (Figure 1). Urdaibai and Txingudi are both coastal tidal marshes, located in estuarine areas, while Adour is a freshwater marsh situated near the river La Nive.

In general, the *Acrocephalus* warblers considered in this study originate from western–eastern Europe and spend the winter in tropical West Africa (Cantos 1998, Zwarts *et al.* 2009, Arizaga, 2010). The only *Acrocephalus* species present in the southeast Bay of Biscay as a breeding bird is the Reed Warbler (e.g. Aierbe *et al.* 2001). However, during migration period, the amount of local birds is marginal compared with the bulk of true migrants. The other *Acrocephalus* species are true migrants.

Time and data collection

Given that the study was chiefly focused on the *Acrocephalus* warblers, the sampling period took place from 1 August to 15 September 2011 for autumn migration and in April 2012 (up to 10 May at Urdaibai and Txingudi) for spring migration (Figure 2). In both cases the dates were selected to coincide with the peak passage of *Acrocephalus* warblers in the region (Arizaga 2010).

Birds at each site were captured with mist nets that were placed at the same site and in the same number during the entire sampling period, both in autumn and spring (Table 1). Nets were opened daily at dawn for 4 hours. In case of poor weather conditions (rain, very high tide or very strong wind), the sampling was suspended (Table 1). This happened more often in spring (up to 15 non-sampling days at Urdaibai) than in autumn

Table 1. Description of sampling sites and effort. The number of simultaneous sampling days in autumn was 42 and in spring 13. The autumn sampling period lasted from 01.08.2011 to 15.09.2011 (46 days), while the spring sampling period lasted from 01.04.2012 to 10.05.2012 (40 days), except at Adour, where the study finished on 30.04.2012 (30 days). The sampling effort at each site was kept constant in both autumn and spring: Adour, 216 linear meters of mist nets; Txingudi, 204 m; Urdaibai, 144 m.

Descripció dels llocs de mostreig i l'esforç dut a terme en cadascun d'ells. El nombre de dies d'anellament en comú va ser 42 a la tardor i 13 a la primavera. El període d'anellament a la tardor va anar de l'01.08.2011 al 15.09.2011 (46 dies), mentre que a la primavera va ser de l'01.04.2012 al 10.05.2012 (40 dies), excepte a Adour, on l'estudi va finalitzar el 30.04.2012 (30 dies). L'esforç es va mantenir constant a cada lloc, tant a la primavera com a la tardor: Adour, 216 m lineals de xarxa; Txingudi, 204 m; Urdaibai, 144 m.

Site (Code) Lloc (Codi)	Sampling days Dies de mostreig	Non-sampling days Dies sense mostreig	Days with no captures Dies sense captures
Adour			
Autumn Tardor	44	2	0
Spring Primavera	25	5	0
Txingudi			
Autumn Tardor	42	4	0
Spring Primavera	26	12	2
Urdaibai			
Autumn Tardor	45	1	0
Spring Primavera	24	15	1

(up to four non-sampling days at Txingudi), partly due to the very wet spring of 2012.

Since the study was partially aimed at discovering how Aquatic Warblers use our wetlands, all three sampling sites were equipped with recordings of the song of a male of Aquatic Warbler (one recording per 36 linear meters of mist nets). This protocol is used in France to determine the use of French wetlands as stopover sites for this species (Julliard *et al.* 2006) and in our case was used both in autumn and spring. It should be added that the use of playbacks in spring is probably not as efficient as in autumn (Poulin *et al.* 2010).

Once captured, birds were ringed (or the ring was read if already ringed). We also measured body mass (0.1 g accuracy) and wing length (± 0.5 mm, method III as described by Svensson 1996).

Data analyses

During migration periods, a large number of migrants may pass through an area in just a few

days. Thus, we only used for analysis those days on which sampling was carried out at the three sites simultaneously, that is, we did not take into account the days on which the sampling was suspended in one or two of the three sampling sites. This was done to avoid sampling a peak in passage at just one site, for example, on a day (or days) on which the two other sites did not open their nets. In the end, we had 42 (out of 46) common sampling days in autumn and 13 common sampling days in spring (out of 30). At each site, we only considered each bird once per sampling day (when the date was the time unit for the analyses) or period (when the period was the time unit for the analyses).

First, we checked whether the number of captures of *Acrocephalus* warblers (standardized by 100 linear meters of mist nets/day) differed between the sites and between periods (autumn/spring). Although the standardized number of captures fitted a normal distribution (K-S test, $P > 0.05$), we observed that the over-dispersion of the data was still large ($SD/mean > 0.48$). Therefore, we used a Friedman test to see wheth-

er the amount of captures varied between sites within each period.

In terms of the proportion of recaptures of *Acrocephalus* warblers, we focus here on the Sedge Warbler, as it was the only one of the three species whose sample size was sufficiently high (>10 captures/site/period) to analyze whether the proportion of recaptures varied between periods. We conducted a chi-square test for each site to test whether the proportion of recaptures differed between periods. A higher proportion of recaptures was considered to indicate that there was a higher proportion of migrants deciding to stay at one site for longer. This is a simple, direct analytical approach for estimating the use of a site by migrants in terms of stopover duration.

The fuel load of migrants is usually stored as fat (Salewski *et al.* 2009) and generally during migration heavier birds are carrying more fuel. Accordingly, a comparison of body mass (after controlling for body size) at sites is sufficient for understanding how birds use these sites to gain fuel (e.g. Schaub & Jenni 2000). We conducted an ANOVA on body mass with wing length as a covariate (used to control body mass for body size) and site and period (this latter only when sample size was sufficiently high, i.e. >10 captures/site/period) as factors. This

was done for all three *Acrocephalus* species. We only considered the first capture event for each bird at each site and period, and only birds with data for wing length and body mass.

Results

Considering only (i) the days when the sampling was carried out at all three sites and (ii) each bird once per site and period, we captured 3,060 birds in total in autumn (Urdaibai, 739; Txingudi, 1,235; Adour, 1,086) and 486 birds in spring (Urdaibai, 81; Txingudi, 111; Adour, 294) (see Appendix I). Overall, we captured four *Acrocephalus* species: Eurasian Reed (58.0% of *Acrocephalus* warblers, autumn and spring pooled), Sedge (39.8%), Aquatic (2.1%) and Great Reed Warbler (0.1%).

The standardized number of captures for all the *Acrocephalus* warblers did not differ between sites in autumn (Friedman test: $\chi^2 = 5.378$, $P = 0.068$; Figure 3). In spring, however, captures varied between sites (Friedman test: $\chi^2 = 8.222$, $P = 0.016$; Figure 3), with the greatest number of captures at Adour.

At Urdaibai and Txingudi, where the study was prolonged for 10 days until 10 May, the number of captures was observed to decrease rather than increase in relation to April (P values for Txingudi and Urdaibai: $P > 0.05$; Figure 4).

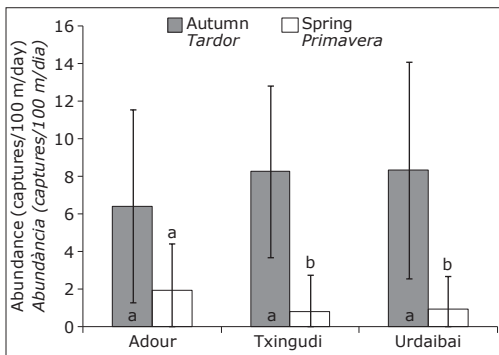


Figure 3. Mean (\pm SD) number of standardized captures (captures/100 m/day) of *Acrocephalus* warblers in three wetlands in the southeast of the Bay of Biscay during autumn and spring migration. In each period, the same letters lump sites for which no significant differences were detected with an *a posteriori* Wilcoxon test.

Nombre mitjà (\pm DE) de captures estandarditzades (captures/100 m/dia) de boscarles del gènere Acrocephalus a tres zones humides del sud-est del golf de Biscaia durant la migració de tardor i primavera. Dintre de cada període, les mateixes lletres indiquen llocs per als quals no van haver diferències significatives mitjançant un test a posteriori de Wilcoxon.

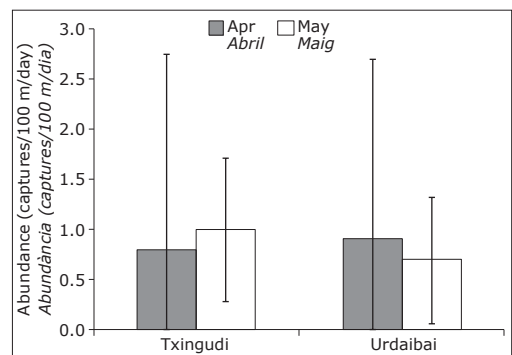


Figure 4. Mean (\pm SD) standardized number of captures (captures/100 m/day) of *Acrocephalus* warblers captured at Txingudi and Urdaibai in April and the first ten days of May.

Nombre mitjà (\pm DE) de captures estandarditzades (captures/100 m/dia) de boscarles del gènere Acrocephalus capturades a Txingudi i Urdaibai durant l'abril i la primera desena de maig.

Table 2. Percentage of recaptures (i.e. migrant birds recaptured once or more often after being ringed at each site as a percentage of all the captures – in brackets) of Sedge Warblers. The proportion of recaptures in the second row of the spring migration period was calculated taking into account all the sampling days at each site in April. Each bird was considered only once per site and period. *Total sampling days in spring: Adour = 25; Txingudi = 20; Urdaibai = 19.

*Percentatge de recaptures de boscarles dels joncs (individus migrants recapturats un o més cops després d'ésser anellats a cada lloc en relació al total de captures –entre parèntesi). El percentatge de recaptures de la segona filera a la migració de primavera es va calcular considerant tots els dies de mostreig a cada lloc a l'abril. Cada ocell es va considerar només un cop a cada lloc i període. *Nombre total de dies de mostreig a la primavera: Adour = 25; Txingudi = 20; Urdaibai = 19.*

Site Lloc	Autumn Tardor	Spring Primavera	χ^2	P
Adour	0.5% (183)	3.0% (33) 4.1% (51)*	1.880 3.590	0.283 0.121
Txingudi	31.4% (220)	0% (18) 2.5% (41)*	7.950 14.732	0.005 <0.001
Urdaibai	33.1% (130)	0% (11) 8.3% (13)*	5.235 3.575	0.034 0.110

Sedge Warblers were recaptured far less in spring than in autumn, except at Adour, where recaptures were also rare in autumn (Table 2). In spring, however, adverse weather obliged us to discard many sampling days and we only considered for analysis those days on which sampling was carried out simultaneously at the three sampling sites. Since this methodological approach may reduce

the number of recaptures (a given bird will be less likely to be recaptured if we remove sampling days), we recalculated the proportion of recaptures at each locality using all the sampling days at each site in April and obtained a similar pattern (Table 2).

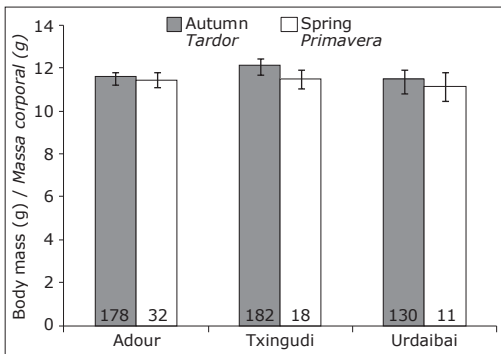


Figure 5. Body mass ($\pm 95\%$ CI) of Sedge Warblers during autumn and spring migration in 2011 and 2012, respectively, at three sampling sites in the southeast of the Bay of Biscay. Sample size is shown at the bottom of the bars. These sample sizes differ from those in Appendix I because some birds did not have their body mass or wing length recorded.

Massa corporal ($\pm 95\%$ IC) de les boscarles dels joncs durant la migració de tardor i primavera de 2011 i 2012, respectivament a tres llocs de mostreig del sud-est del golf de Biscaia. Els números a la part de baix de les columnes indiquen el nombre d'individus (les diferències respecte als valors mostrats a l'Apèndix I són a causa que no es van poder mesurar la massa i la longitud de l'ala a tots els individus).

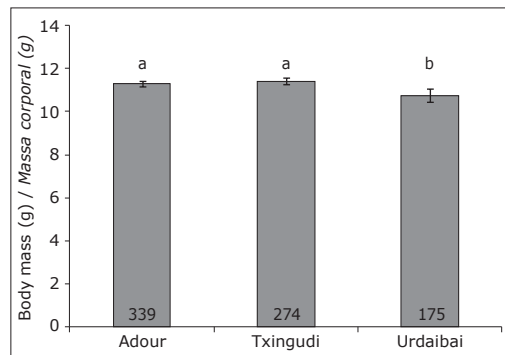


Figure 6. Body mass ($\pm 95\%$ CI) of Reed Warblers during autumn migration in 2011 at three sampling sites from the southeast of the Bay of Biscay. Sample size is shown at the bottom of the bars. These sample sizes differ from those in Appendix I because some birds did not have their body mass or wing length recorded. The letters above the bars group the sites for which there were no significant differences according to a Duncan *a posteriori* test.

*Massa corporal ($\pm 95\%$ IC) de les boscales de canyar durant la migració de tardor de 2011 a tres llocs de mostreig del sud-est del golf de Biscaia. Els números a la part baixa de les columnes indiquen el nombre d'individus (les diferències respecte als valors mostrats a l'Apèndix I són a causa que no es van poder mesurar la massa i la longitud de l'ala a tots els individus). Les lletres sobre les barres agrupen aquells llocs entre els quals no hi va haver diferències significatives segons el test *a posteriori* de Duncan.*

Sedge Warblers' body mass did not differ in relation to the period and site (Figure 5; Covariate wing length: $F_{1,551} = 27.330$, $P < 0.001$; Period, $F_{1,551} = 2.288$, $P = 0.131$; Site, $F_{2,551} = 0.559$, $P = 0.572$; Period \times Site, $F_{2,551} = 0.375$, $P = 0.687$). In Eurasian Reed Warblers, body mass in autumn was found to be lower at Urdaibai than at the other two sites (Figure 6; Covariate wing length: $F_{1,788} = 92.927$, $P < 0.001$; Site, $F_{2,788} = 3.098$, $P = 0.046$). In this case the small sample size did not allow us to check for variations between the two periods. The sample size was also too small for the other two species.

Discussion

Using data from these three wetlands situated in the southeast of the Bay of Biscay, we aimed to compare how *Acrocephalus* warbler species use these sites during autumn and spring migrations *en route* to or from Africa, respectively. A key point for the proper interpretation of our data was the representativeness of the captures in relation to the amount of migrants that may not have been captured (despite stopping) or may not have landed (despite flying over) in the southeast of the Bay of Biscay. The reasonably high number of captures of *Acrocephalus* warblers in autumn suggests that at least in this season captures were likely to be representative of all or most *Acrocephalus* deciding to land (Schaub & Jenni 2000, 2001). The fact that *Acrocephalus* warblers are captured very commonly in other stopover sites in spring (Barriocanal *et al.* 2002, Gargallo *et al.* 2011) suggests that our captures were also representative for the real number of migrants stopping over in the southeast of the Bay of Biscay in this season. Using a recording with the song of a male Aquatic Warbler could also create some biases (i.e. over-estimation) in the number of captures of *Acrocephalus* warblers and, in particular, of the Aquatic Warbler (Julliard *et al.* 2006). Furthermore, recordings may have been effective in autumn but not in spring (Poulin *et al.* 2010), which could create an over-estimation of captures in autumn. A possible solution would be to avoid the use of recordings in both autumn and spring to ensure that the data is more comparable between periods.

The *Acrocephalus* warblers tended to be

much more numerous during the autumn than during the spring migration period. This result must be interpreted bearing in mind the fact that the sampling was done in August–mid-September for the autumn migration period and in April for the spring migration period. Therefore, our data will be applicable for the majority of long-distance migrants that overwinter in tropical Africa (including *Acrocephalus* warblers) and stopover at wetlands along the southeastern coast of the Bay of Biscay, but not for the short-distance migrants that overwinter north of the Sahara and migrate later in autumn and, in some cases, earlier in spring (Tellería *et al.* 1999, Arizaga *et al.* 2010c). Although populations are much less numerous in spring than in autumn due to the high first-year mortality rate (Newton 1998), our findings cannot be attributed to this fact alone (see below for further details).

We found the Sedge Warbler to be one of the three most abundant passerines at all three sites in both autumn and spring (Appendix I), thereby supporting the idea that the sampling was adjusted to the species' habitat and passage period throughout the whole area. This is coherent with the fact that this bird is one of the main components of reed bed bird assemblages during autumn migration period in this region (Arizaga *et al.* 2009), and confirms that the same rule applies for the spring migration period. The proportion of Sedge Warblers that take a more easterly route through Iberia in spring than in autumn does not vary between these two periods, thereby indicating that, overall, this species uses the same routes in autumn and spring, at least in Iberia (Cantos 1998). Given this, our results are compatible with the fact that, even if they pass over the southeast of the Bay of Biscay in spring, Sedge Warblers perform longer flights (thus each individual bird stops over at fewer sites), have shorter stopovers if they land (see below for further details), and, even if they do land, do not resume their migration until the night (Jenni-Eiermann *et al.* 2011).

Eurasian Reed Warblers, by contrast, were very scarce in spring and only occupy a marginal position in the passerine assemblage. This finding clearly differs from the results obtained in autumn. In our opinion, the most likely explanation is that Reed Warblers in spring tend to take more easterly migratory routes (Mediterranean and the Balearics in spring vs.

Atlantic in autumn) when crossing Iberia on their way to their breeding areas (Cantos 1998); unlike Sedge Warblers, their passage tends to be later in spring (Gargallo *et al.* 2011) and so it is likely that the bulk of Reed Warblers pass through the southeast Bay of Biscay after mid-May. Thus, some non-breeding Reed Warblers captured in June 2006 at Txingudi could still be on migration to their breeding grounds (Arizaga *et al.* 2010b). Data obtained in May at a constant effort site used to survey breeding Reed Warblers at Txingudi (J. Arizaga, unpubl. data), however, suggest small/moderate numbers of Reed Warblers do migrate through the region as suggested by the observations from the Adour marshes (P. Fontanilles, unpubl. data).

Aquatic Warblers were captured at all sites but only in autumn; most birds were caught at Adour. Almost 90% of the Aquatic Warblers caught in Spain in spring have been captured in April. The lack of captures of Aquatic Warbler at our sites was not due to the fact that the sampling period was not adjusted to the species' passage period; rather, this species takes a more easterly route when crossing Iberia *en route* to its breeding grounds in eastern Europe (Atienza *et al.* 2001), much as has been reported for the Eurasian Reed Warblers.

Great Reed Warblers were very scarce and were caught only in autumn and thus should be considered as rare birds in the southeast of the Bay of Biscay in this season. This scarcity may in part be due to the fact that this species is relatively much more uncommon on the coast of western Europe than in inland areas and further to the east (Cramp 1992). Thus, most of this species' populations from central-western Europe will probably migrate along a more Mediterranean route to or from their wintering areas in tropical Africa (Cantos 1998). In addition, it is also possible that a large number of birds may gain in or near their breeding areas all the fuel they require to cross the Sahara and therefore have no need for the possible (potential) stop-over sites situated south of their breeding ranges (Cramp 1992).

In Sedge Warblers, we obtained a large sample size that enabled us to properly estimate whether the proportion of recaptures differed between periods. Alternative methodologies such as the use of the Cormack-Jolly-Seber models (Schaub *et al.* 2001) have been revealed

to be better since they allow for survival (here re-interpreted as the staying probability) and recapture probabilities to be estimated separately. The use of Cormack-Jolly-Seber models, however, requires a relatively large amount of data. Unfortunately, this was not possible in our case. We observed at Txingudi and Urdaibai that ca. 25% of birds were recaptured in autumn, whilst no recaptures were obtained in spring. At Adour, by contrast, a negligible proportion of recaptures (<3%) was obtained both in autumn and spring. Overall, in spring only a marginal fraction of Sedge Warblers decide to stay in the sites for more than one or just a few days, thereby supporting the idea that migration is faster in spring than in autumn (Newton 2008). The Adour, however, seemed to be different due to the lack of recaptures in autumn. The causes explaining these results remain obscure and we can do no more than suggest possible hypotheses. For example, food availability or other factors may make the site at Adour more attractive for birds than at Txingudi or Urdaibai.

Body mass in Sedge Warblers did not differ between periods and sites and so the fuel loads of Sedge Warblers passing through our area can be considered to be similar. According to a previous study, these fuel loads would be sufficient to cover (estimating a single flight with no stopovers) a distance of 1,500–2,000 km (Arizaga & Barba 2009a), which would allow Sedge Warblers to reach the north of the Sahara in autumn without refuelling. In spring, therefore, Sedge Warblers would be able to reach their breeding quarters along the coast of France, central-western Europe and the British Isles without stopping. The small percentage of birds that seem to decide to stop over in the southeast of the Bay of Biscay in spring suggests that these birds accumulate enough fat further south to reach their breeding areas without refuelling (Arizaga & Barba 2009a).

In conclusion, the spring migration of *Acrocephalus* warblers in the southeast of the Bay of Biscay is much weaker than in autumn. The remarkable scarcity of Eurasian Reed Warblers in spring may be due in part to the fact that they tend to pass through later than the other two species, although, even despite this fact, its passage was still lower than in autumn. In Sedge Warblers, where the sample size was sufficiently high, the few birds that did stop over

in the sampled marshes were also observed to stay apparently for less time in spring than in autumn, a finding that should be properly tested with Cormack-Jolly-Seber models.

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Resum

Ecologia en els llocs de parada migratòria del gènere *Acrocephalus* a les maresmes del Cantàbric sud-oriental durant el període de pas post- i prenupcial

Comprendre com les espècies del gènere *Acrocephalus* fan servir els aiguamolls costaners del Cantàbric sud-oriental durant el període de pas migratori és bàsic des del punt de vista de la seva conservació i gestió. L'objectiu d'aquest treball va ser explorar si les espècies del gènere *Acrocephalus* utilitzen la regió a la primavera d'igual manera que a la tardor. Per a això, es van emprar dades obtingudes en tres estacions d'anellament situades en tres aiguamolls costaners (estuàries d'Adour, Txingudi i Urdaibai) durant la tardor de 2011 i la primavera de 2012. En conjunt, el pas de primavera va ser notablement inferior que el de tardor, quan es van obtenir més captures per dia. El baix nombre de captures de Boscarla de canyar *A. scirpaceus* a la primavera va ser a causa d'un pas més tardà que en d'altres espècies com la Boscarla dels joncs *A. schoenobaenus* i la Boscarla d'aigua *A. paludicola*. No obstant això, si es consideren altres dades addicionals, l'escassetat de Boscarla de canyar no només s'explicaria per aquesta circumstància. A la primavera la Boscarla dels joncs tindria, aparentment, períodes d'estada més curts que a la tardor, però una quantitat de reserves semblant.

Resumen

Ecología en puntos de parada migratoria en el género *Acrocephalus* en marismas del Cantábrico sudoriental durante el periodo de paso pos- y prenupcial

Comprender cómo las especies del género *Acrocephalus* utilizan las marismas costeras del Cantábrico sudoriental durante el periodo de paso migratorio es básico desde el punto de vista de su conservación y gestión. El objetivo de este trabajo fue explorar si las especies del género *Acrocephalus* utilizan la región en primavera de manera igual al otoño. Para ello, se emplearon datos obtenidos en tres estaciones de anillamiento situadas en tres marismas costeras (estuàries de Adour, Txingudi y Urdaibai) en el otoño de 2011 y la primavera de 2012. En conjunto, el paso de primavera fue notablemente más débil que el de otoño, donde se obtuvieron más capturas por día. El bajo número de capturas de Carricero común *A. scirpaceus* en primavera pudo explicarse a un paso más tardío que especies como el Carricero común *A. schoenobaenus* y el Carricero cejudo *A. paludicola*. No obstante, si se consideran otros datos adicionales, la escasez de Carricero común no se explicaría sólo por esta circunstancia. En primavera el Carricero común tendría, aparentemente, periodos de estancia más cortos que en otoño, pero una cantidad de reservas similar.

References

- Aierbe, T., Olano, M. & Vázquez, J. 2001. Atlas de las aves nidificantes de Gipuzkoa. *Munibe* 52 (Supl.).
- Arizaga, J. 2010. Análisis de recapturas de carriceros (*Acrocephalus* spp.) en Txingudi: ruta migratoria, tiempo de paso y velocidades migratorias. *Munibe* 58: 197–209.
- Arizaga, J., Alonso, D., Fernández, E., Fernández, I., Martín, D. & Vilches, A. 2009. La laguna de Badina de Escudera (Navarra): características de la comunidad de aves paseriformes. *Munibe* 28 (Supl.).
- Arizaga, J. & Barba, E. 2009a. Fuel load and flight ranges of blackcaps *Sylvia atricapilla* in northern Iberia during the autumn and spring migrations. *Curr. Zool.* 55: 401–410.
- Arizaga, J. & Barba, E. 2009b. Importance of sampling frequency to detect differential timing of migration: a case study with Blackcaps *Sylvia atricapilla*. *Ardea* 97: 297–304.
- Arizaga, J., Barba, E., Alonso, D. & Vilches, A. 2010a. Stopover of bluethroats (*Luscinia svecica cyanecula*) in northern Iberia during the autumn migration period. *Ardeola* 57: 69–85.
- Arizaga, J., Mendiburu, A. & Alonso, D. 2010b. Non-breeding reed warblers *Acrocephalus scirpaceus* (Hermann, 1804) in June in southern Europe:

- local or still migrating birds? *Belg. J. Zool.* 140: 74–76.
- Arizaga, J., Mendiburu, A., Aranguren, I., Asenjo, I., Cuadrado, J.E., Díez, E., Elosegí, Z., Herreiro, A., Jauregi, J.I., Pérez, J.I. & Sánchez, J. M.** 2010c. Estructura y evolución de la comunidad de passeriformes a lo largo del ciclo anual en el Parque Ecológico de Plaiaundi (marismas de Txingudi, Guipúzcoa). *Ecología* 23: 153–164.
- Arizaga, J., Sánchez, J.M., Díez, E., Cuadrado, J.E., Asenjo, I., Mendiburu, A., Jauregi, J.I., Herreiro, A., Elosegí, Z., Aranguren, I., Andueza, M. & Alonso, D.** 2011. Fuel load and potential flight ranges of passerine birds migrating through the western edge of the Pyrenees. *Acta Ornithol.* 46: 19–28.
- Atienza, J.C., Pinilla, J. & Justribó, J.H.** 2001. Migration and conservation of the Aquatic Warbler (*Acrocephalus paludicola*) in Spain. *Ardeola* 48: 197–208.
- Barriocanal, C., Montserrat, D. & Robson, D.** 2002. Influences of wind flow on stopover decisions: the case of the reed warbler *Acrocephalus scirpaceus* in the Western Mediterranean. *Int. J. Biometeorol.* 46: 192–196.
- Bibby, C.J. & Green, R.E.** 1981. Migration strategies of reed and sedge warblers. *Ornis Scand.* 12: 1–12.
- Biebach, H.** 1990. Strategies of trans-Saharan migrants. In Gwinner, E. (ed.): *Bird migration*. Pp. 352–367. Berlin: Springer Heidelberg.
- Caillat, M., Dugué, H., Leray, G., Gentric, A., Pourreau, J., Julliard, R. & Yésou, P.** 2005. Résultat de dix années de baguage de fauvettes paludicoles *Acrocephalus* sp. dans l'Estuaire de la Loire. *Alauda* 73: 375–388.
- Cantos, F.J.** 1998. Patrones geográficos de los movimientos de silvídos transaharianos a través de la Península Ibérica. *Ecología* 12: 407–411.
- Cramp, S.** 1992. *The Birds of the Western Palearctic*. Vol. 6. Oxford: Oxford University Press.
- Chenaval, N., Lorrillière, R., Dugué, H. & Doxa, A.** 2011. Phénologie et durée de halte migratoire de quatre passereaux paludicoles en migration post-nuptiales en estuaire de La Loire. *Alauda* 79: 149–156.
- Dierschke, V. & Delingat, J.** 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. *Behav. Ecol. Sociobiol.* 50: 535–545.
- Ellegren, H.** 1991. Stopover ecology of autumn migrating bluethroats *Luscinia svecica svecica* in relation to age and sex. *Ornis Scand.* 22: 340–348.
- Fontanilles, P., Borie, M., Dufresnes, L., Fourcade, J.-M., Lapios, J.M. & Thouy, P.** 2010. Bilan du baguage des passereaux migrateurs sur les barthes de la Nive (Pyrénées-Atlantiques) en 2009. *Le Casseurd'os* 10: 75–79.
- Gargallo, G., Barriocanal, C., Castany, J., Clarabuch, O., Escandell, R., López, G., Rguibi, H., Robson, D. & Suárez, M.** 2011. *Spring bird migration in the Western Mediterranean: results from the Piccole Isole Project*. Monografías del Museu de Ciències Naturals 6. Barcelona: Museu de Ciències Naturals.
- González, J.V., Otero, B.N., Muñoz, B. & Gómez, R.** 2007. *Estudio de la avifauna en el porreo de Villaverde (Ría de Villaviciosa, Asturias)*. Gijón: Sociedad Asturiana de Historia Natural y Ecología.
- Grandío, J.M.** 1997. Sedimentación y fenología otoñal de tres especies de curruca (*Sylvia* spp.) en el extremo occidental del Pirineo. *Ardeola* 44: 163–171.
- Grandío, J.M.** 1998. Comparación del peso y su incremento, tiempo de estancia y de la abundancia del carricerín común (*Acrocephalus schoenobaenus*) entre dos zonas de la marisma de Txingudi (N de España). *Ardeola* 45: 137–142.
- Jenni-Eiermann, S., Almasi, B., Maggini, I., Salewski, V., Bruderer, B., Liechti, F. & Jenni, L.** 2011. Numbers, foraging and refuelling of passerine migrants at a stopover site in the western Sahara: diverse strategies to cross a desert. *J. Ornithol.* 152: S113–S128.
- Julliard, R., Bargain, B., Dubos, A. & Jiguet, F.** 2006. Identifying autumn migration routes for the globally threatened Aquatic Warbler *Acrocephalus paludicola*. *Ibis* 148: 735–743.
- Lavee, D., Safriel, U.N. & Meilijson, I.** 1991. For how long do trans-Saharan migrants stop over at an oasis? *Ornis Scand.* 22: 33–44.
- Mendiburu, A., Aranguren, I., Elosegí, Z., Jauregi, J.I., Sánchez, J.M., Cuadrado, J.F., Alonso, D. & Arizaga, J.** 2009. Resultados de la primera campaña de anillamiento en el paso migratorio posnupcial en la vega de la regata de Jaizubia (marismas de Txingudi). *Revista de Anillamiento* 23: 26–34.
- Newton, I.** 1998. *Population limitation in birds*. London: Academic Press.
- Newton, I.** 2008. *The migration ecology of birds*. London: Academic Press.
- Poulin, B., Duborper, E. & Lefebvre, G.** 2010. Spring stopover of the globally threatened Aquatic Warbler *Acrocephalus paludicola* in Mediterranean France. *Ardeola* 57: 167–173.
- Salewski, V., Kéry, M., Herremans, M., Liechti, F. & Jenni, L.** 2009. Estimating fat and protein fuel from fat and muscle scores in passerines. *Ibis* 151: 640–653.
- Schaub, M. & Jenni, L.** 2000. Body mass of six long-distance migrant passerine species along the autumn migration route. *J. Ornithol.* 141: 441–460.
- Schaub, M. & Jenni, L.** 2001. Stopover durations of three warblers species along their autumn migration route. *Oecologia* 128: 217–227.
- Schaub, M., Pradel, R., Jenni, L. & Lebreton, J.D.** 2001. Migrating birds stop over longer than usually thought: An improved capture-recapture analysis. *Ecology* 82: 852–859.
- Svensson, L.** 1996. *Guía para la identificación de los passeriformes europeos*. Madrid: SEO/BirdLife.
- Tellería, J.L., Asensio, B. & Díaz, M.** 1999. *Aves Ibéricas. II. Paseriformes*. Madrid: Reyero Ed..
- Zwarts, L., Bijlsma, R.G., van der Kamp, J. & Wymenga, E.** 2009. *Living on the edge: Wetlands and birds in a changing Sahel*. Zeist: KNNV Publishing.

Appendix I. Standardized (captures/100 m/day) number of passerines captured (each bird considered only once) at each sampling site (Adour, Txingudi, Urdaibai) during autumn and spring migration. Only common sampling days are considered here. The absolute number of captures at each site is shown in brackets.

Nombre estandarditzat (captures/100 m/dia) de passeriformes capturats (cada ocell considerat només un cop) a cada lloc de mostreig (Adour, Txingudi, Urdaibai) durant la migració de tardor i primavera. Només s'han considerat els dies comuns de mostreig. Entre parèntesis es mostren els nombres absoluts de captures.

Species Espècies	Autumn Tardor			Spring Primavera		
	Adour	Txingudi	Urdaibai	Adour	Txingudi	Urdaibai
<i>A. arundinaceus</i>	0.01 (1)	0 (0)	0.02 (1)	0 (0)	0 (0)	0 (0)
<i>A. paludicola</i>	0.21 (19)	0.05 (4)	0.13 (8)	0 (0)	0 (0)	0 (0)
<i>A. schoenobaenus</i>	2.02 (183)	2.57 (220)	2.15 (130)	0.36 (33)	0.21 (18)	0.18 (11)
<i>A. scirpaceus</i>	3.80 (345)	3.72 (319)	2.89 (175)	0.20 (18)	0.04 (3)	0.10 (6)
<i>A. caudatus</i>	0.02 (2)	0.05 (4)	0.20 (12)	0 (0)	0 (0)	0 (0)
<i>A. trivialis</i>	0.01 (1)	0.01 (1)	0 (0)	0 (0)	0.01 (1)	0 (0)
<i>C. carduelis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.05 (3)
<i>C. brachydactyla</i>	0.01 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>C. cetti</i>	0.40 (36)	0.20 (17)	0.35 (21)	0.06 (5)	0 (0)	0.02 (1)
<i>C. juncidis</i>	0 (0)	0.04 (3)	0.69 (42)	0 (0)	0 (0)	0.08 (5)
<i>C. caeruleus</i>	0.31 (28)	0.33 (28)	0.23 (14)	0 (0)	0 (0)	0 (0)
<i>E. schoeniclus</i>	0 (0)	0 (0)	0 (0)	0.02 (2)	0.02 (2)	0.03 (2)
<i>E. rubecula</i>	0.73 (66)	0.04 (3)	0.15 (9)	0.55 (50)	0.11 (9)	0.07 (4)
<i>F. hypoleuca</i>	0.23 (21)	0.12 (10)	0.12 (7)	0.02 (2)	0.04 (3)	0 (0)
<i>F. coelebs</i>	0 (0)	0 (0)	0.02 (1)	0 (0)	0 (0)	0 (0)
<i>H. polyglotta</i>	0.11 (10)	0.37 (32)	0.12 (7)	0.03 (3)	0.02 (2)	0 (0)
<i>H. rustica</i>	0 (0)	0.02 (2)	0 (0)	0 (0)	0 (0)	0.12 (7)
<i>J. torquilla</i>	0.04 (4)	0.04 (3)	0 (0)	0 (0)	0.01 (1)	0 (0)
<i>L. collurio</i>	0.09 (8)	0.02 (2)	0.07 (4)	0 (0)	0 (0)	0 (0)
<i>L. luscinioides</i>	0.01 (1)	0.01 (1)	0.02 (1)	0 (0)	0 (0)	0 (0)
<i>L. naevia</i>	0.49 (44)	0.02 (2)	0.07 (4)	0.03 (3)	0 (0)	0 (0)
<i>L. megarhynchos</i>	0.30 (27)	0.04 (3)	0.05 (3)	0.08 (7)	0.02 (2)	0 (0)
<i>L. svecica</i>	0.28 (25)	0.85 (73)	0.76 (46)	0.07 (6)	0.02 (2)	0.12 (7)
<i>M. alba</i>	0 (0)	0.04 (3)	0 (0)	0 (0)	0 (0)	0 (0)
<i>M. flava</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.02 (1)
<i>M. striata</i>	0.02 (2)	0.01 (1)	0.02 (1)	0 (0)	0.01 (1)	0 (0)
<i>O. oenanthe</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.02 (1)
<i>P. major</i>	0.14 (13)	0.07 (6)	0.12 (7)	0.03 (3)	0 (0)	0 (0)
<i>P. domesticus</i>	0 (0)	0.76 (65)	0.03 (2)	0 (0)	0.07 (6)	0 (0)
<i>P. montanus</i>	0 (0)	0.08 (7)	0.03 (2)	0 (0)	0.02 (2)	0 (0)
<i>P. ochrurus</i>	0 (0)	0.01 (1)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. phoenicurus</i>	0.03 (3)	0 (0)	0 (0)	0.10 (9)	0.01 (1)	0 (0)
<i>P. collybita</i>	0.06 (5)	0 (0)	0 (0)	0.09 (8)	0.07 (6)	0.03 (2)
<i>P. ibericus</i>	0 (0)	0.01 (1)	0.08 (5)	0 (0)	0.05 (4)	0 (0)
<i>P. trochilus</i>	0.43 (39)	3.09 (265)	3.27 (198)	0.12 (11)	0.25 (21)	0.28 (17)
<i>P. modularis</i>	0.01 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>R. ignicapilla</i>	0 (0)	0 (0)	0.03 (2)	0 (0)	0 (0)	0 (0)
<i>S. rubetra</i>	0.01 (1)	0.02 (2)	0.13 (8)	0.01 (1)	0.01 (1)	0.02 (1)
<i>S. rubicola</i>	0.01 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>S. unicolor</i>	0 (0)	0.06 (5)	0 (0)	0 (0)	0 (0)	0 (0)
<i>S. vulgaris</i>	0 (0)	1.30 (111)	0.02 (1)	0 (0)	0 (0)	0 (0)
<i>S. atricapilla</i>	0.87 (79)	0.01 (1)	0.05 (3)	1.19 (108)	0.20 (17)	0.03 (2)
<i>S. borin</i>	0.41 (37)	0.18 (15)	0.02 (1)	0.01 (1)	0 (0)	0.03 (2)
<i>S. communis</i>	0.35 (32)	0.07 (6)	0.33 (20)	0.14 (13)	0.07 (6)	0.12 (7)
<i>T. troglodytes</i>	0.12 (11)	0.01 (1)	0.07 (4)	0.07 (6)	0 (0)	0 (0)
<i>T. merula</i>	0.36 (33)	0.13 (11)	0 (0)	0.04 (4)	0.01 (1)	0.02 (1)
<i>T. philomelos</i>	0.08 (7)	0.08 (7)	0 (0)	0.01 (1)	0.02 (2)	0.02 (1)