

– Parc naturel régional de Brière –

# Séminaire

Passereaux migrateurs des zones humides,

le cas du **Phragmite aquatique**

1<sup>er</sup> et 2 février 2013



Photo Philippe Zen





# ALAUDA

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### SÉMINAIRE « PASSEREAUX MIGRATEURS DES ZONES HUMIDES, LE CAS DU PHRAGMITE AQUATIQUE » 1<sup>er</sup> ET 2 FÉVRIER 2013

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Sous la responsabilité et la coordination de Matthieu MARQUET

#### LISTE DES CONTRIBUTIONS

- **Luc BARBIER:** Allocution d'introduction à la journée d'échanges autour du Phragmite aquatique (*Acrocephalus paludicola*) acronymiquement appelé ACROLA.
- **Pierre NICOLAU-GUILLAUMET:** Les migrations des oiseaux.
- **Matthieu MARQUET, Patrick BONNET, Emmanuel SÉCHET, Robin JULIEN, Félix BÉCHEAU et Christian KERBIRIOU:** La Brière, un site de halte migratoire post-nuptiale d'importance pour le Phragmite aquatique (*Acrocephalus paludicola*) et éléments d'écologie de l'espèce sur ce site.
- **Julien FOUCHER, Euriel JAGUENET, Marine BOUCAUX, Étienne GIRAUDOT, Eugène ARCHER, Benjamin JEANNEAU, Joanna DZIARSKA-PALAC, Aurélia LACHAUD et Hubert DUGUÉ:** Résultats de 10 ans de suivi du Phragmite aquatique *Acrocephalus paludicola* à la station de baguage de Donges dans l'Estuaire de la Loire.



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■ **Michel LEDARD et Christine BLAIZE:** Le plan national d'actions du Phragmite aquatique (*Acrocephalus paludicola*), enjeux et synthèse nationale.

■ **Franck LATRAUBE et Arnaud LE NEVÉ:** La migration postnuptiale du Phragmite aquatique en région des Pays de la Loire et les habitats fréquentés.



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■ **Géraud RANVIER, Matthieu MARQUET et Thierry MOUGEY:** Quel rôle les Parcs naturels régionaux jouent-ils dans la conservation des haltes migratoires du Phragmite aquatique (*Acrocephalus paludicola*)?

■ **Raphaël MUSSEAU, Valentine HERRMANN et Thomas HÉRAULT:** Stratégies d'occupation spatiale du Phragmite aquatique (*Acrocephalus paludicola*) sur une importante escale migratoire et orientations de gestion des espaces sur un site-clé pour l'espèce.

■ **Philippe FONTANILLES, Benoît LAVAL et Maxime DIRIBARNE:** Sélection des habitats et occupation spatiale du Phragmite aquatique *Acrocephalus paludicola* sur une halte migratoire du Sud-Ouest de la France, mise en place d'une gestion intégrée.

■ **Juan ARIZAGA, Miren ANDUEZA, Ainara AZKONA, Hubert DUGUÉ, Philippe FONTANILLES, Julien FOUCHER, Valentine HERRMANN, Jean M. LAPIOIS, Manuel MENÉNZ, Raphaël MUSSEAU, Edorta UNAMUNO et Paloma PEÓN:** Reed-bed use by the Aquatic Warbler *Acrocephalus paludicola* across the Bay of Biscay during the autumn migration of 2011.

■ **Luc BARBIER:** Discours de clôture.

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Textes réunis par **M. MARQUET**.

## REED-BED USE BY THE AQUATIC WARBLER *Acrocephalus paludicola* ACROSS THE BAY OF BISCAY DURING THE AUTUMN MIGRATION OF 2011

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### Utilisation de la roselière par le Phragmite aquatique *Acrocephalus paludicola* dans le golfe de Gascogne lors de la migration d'automne 2011.

Le Phragmite aquatique est l'un des passereaux les plus menacés dans le monde et le seul avec un risque d'extinction en Europe continentale. Le but de ce travail est de déterminer l'importance des zones humides du golfe de Gascogne pour le Phragmite aquatique, pendant la période de migration post-nuptiale. Pour tester cela nous avons utilisé des données de capture-marquage-recapture récoltées sur des migrants capturés en roselières *Phragmites* spp. sur six sites utilisant un protocole d'échantillonnage commun lors du passage en 2011. Le nombre standardisé de captures a tendance à diminuer du Nord au Sud en France (de 1,8 à 0,3 capture/100 mètres de filets japonais/jour) et il est très faible dans le Nord de la péninsule ibérique (< à 0,2 capture/100 mètre de filets japonais/j). Le pourcentage de captures de Phragmite aquatique par rapport à tout le genre *Acrocephalus* est égal à 1,5 % mais il diffère entre les stations avec des valeurs plus élevées que prévu dans deux zones humides du Sud-Ouest de la France (4,2 % et 3,7 %). La proportion d'oiseaux de première année et le niveau des réserves énergétiques ont tendance à diminuer du Nord au Sud en France (ces analyses n'ont pas été faites pour l'Espagne en raison de la faible grandeur de l'échantillon). Tout ceci est discuté sous le point de vue de l'identification des sites cibles d'escale migratoire pour le Phragmite aquatique et de la stratégie de migration de l'espèce dans le golfe de Gascogne, tout en tenant compte du fait qu'une seule année d'échantillonnage n'a été analysée ici.

**Reed-bed use by the Aquatic Warbler *Acrocephalus paludicola* across the Bay of Biscay during the autumn migration of 2011.** The Aquatic Warbler *Acrocephalus paludicola* is one of the most threatened passerines in the world and the only under risk of extinction in mainland Europe. The goal of this work is to determine the relevance of wetlands of the Bay of Biscay for the Aquatic Warbler, during the autumn migration period. To test this we used ringing data on migrants caught at reedbeds *Phragmites* spp. in six sites using a common sampling protocol, during the autumn passage of 2011. The standardized number of captures tended to decrease from North to South in France (from 1.8 to 0.3 captures/100 m of mist nets/d), and it was very low in northern Iberia (< 0.2 captures/100 m of mist nets/d). The percentage of captures of Aquatic Warbler in relation to all *Acrocephalus* was 1.5% but it differed between stations, with higher-than-expected values at two wetlands from southwestern France (4.2% and 3.7%). The proportion of first-year birds and the mean fuel load tended to decrease from North to South in France (analyses not done for Iberia due to the small sample sizes). All this is discussed under the point of view of the identification of target stopover places for the Aquatic Warbler and its strategy of migration in the Bay of Biscay, considering that a single sampling year was here used.

**Mots clés:** *Acrocephalus paludicola*, Age-ratio, Voies migratoires atlantiques, Marais côtiers, Réserve énergétique, Baguage, Zones humides, Golfe de Gascogne.

**Key words:** *Acrocephalus paludicola*, Age-ratios, Atlantic flyway, Coastal marshes, Fuel load, Ringing, Wetlands, Bay of Biscay (Western France).



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## INTRODUCTION

Wetlands play a fundamental role for the conservation of biodiversity (WELLER, 1999; KEDDY, 2010). They constitute priority ecosystems not only for resident species but also for species, or populations, using these sites temporally, e.g. as stopover sites for birds during migration period.

The East-Atlantic coastal marshes constitute a rosary of wetlands within one of the main migratory ways between Europe and Africa. Such marshes are capital as stopover sites for birds that use them to either rest and/or gain the energy that they need to address with success the next flight bout. The Bay of Biscay and its shores in particular, occupies a remarkable position in this route since it hosts huge numbers of migrant birds in their route to Africa during the autumn migration period, from waterbirds (ARIZAGA *et al.*, 2010; NAVEDO *et al.*, 2010) to passerines (CAILLAT *et al.*, 2005; JULLIARD *et al.*, 2006; MENDIBURU *et al.*, 2009; CHENAVAL *et al.*, 2011).

The Aquatic Warbler *Acrocephalus paludicola* is one of the most threatened passerines in the world and it is reported to stop over periodically in several coastal marshes of the Bay of Biscay (JULLIARD *et al.*, 2006; ARIZAGA *et al.*, 2011b; JIGUET *et al.*, 2011). Although earlier studies have shown that the Aquatic Warbler depends mainly on wetlands from northwestern France to refuel during migration period (JULLIARD *et al.*, 2006), studies carried out in other regions further south have demonstrated that these southern sites also have great importance for the Aquatic Warbler (NETO *et al.*, 2010; JIGUET *et al.*, 2011), thus suggesting that some coastal marshes from the southern part of the Bay of Biscay also have a great value for these birds. The lack of a common

survey method for the entire region, including potential stopovers in northern Iberia (ATIENZA *et al.*, 2001), makes a proper evaluation on the use of these marsh areas hard to carry-out on a large-scale. Accordingly, the relative importance of the entire Bay of Biscay for the Aquatic Warbler remains unknown.

Although the Aquatic Warbler has no preference for reedbeds but rather for wet grasslands (PROVOST *et al.*, 2010), the species has also reported to appear in reedbeds (JULLIARD *et al.*, 2006; NETO *et al.*, 2010; ARIZAGA *et al.*, 2011b). Furthermore, captures in this type of vegetation have been used to identify Aquatic Warblers' target stopover sites during migration period (JULLIARD *et al.*, 2006). In contrast to wet grasslands the reedbeds are much more common across the Bay of Biscay, occupy larger surfaces, so sampling in reedbeds allows us to compare a greater number of potential stopovers for the Aquatic Warbler within this region.

The aim of the present article is to determine the relevance of wetlands of the Bay of Biscay, particularly reedbeds *Phragmites* spp., as stopover and fuelling sites for the Aquatic Warbler. To test this we used ringing data on migrants caught at six sites using a common sampling protocol, during the autumn passage of 2011.

## MATERIAL AND METHODS

### Sampling sites

Data were obtained at six coastal marshes located along the coast of the Bay of Biscay, from Loire, in northwestern France, to Villaviciosa, in northwestern Spain (FIG. 1). These six sites were considered to be representative of coastal





**FIG. 1.**— Location of the six sampling sites where the study was carried out. Abbreviations, as in table I. *Situation des six sites d'échantillonnage où l'étude a été réalisée. Les abbreviations, comme dans le tableau I.*

**TABLE I.**— Sampling sites where the study was carried out, in August 2011 (from 1<sup>st</sup> to 28<sup>th</sup>). Abbreviations: REED, area with reedbeds (proportion) around the mist nets; HERB, herbaceous plants, no reedbeds; BUSH, bushes; TREE, trees; FREE, water and/or mud flats.

*Sites d'échantillonnage où l'étude a été réalisée, en août 2011 (du 1<sup>er</sup> au 28). Abréviations : REED, zone de roselières (proportion) autour des filets japonais ; HERB, plantes herbacées, pas de roselières ; BUSH, buissons ; TREE, arbres ; FREE, eau et/ou les vasières.*

marshes within the study area since all of them have been reported to host great numbers of migrant birds, especially *Acrocephalus* warblers (e.g., GONZÁLEZ *et al.*, 2007; MENDIBURU *et al.*, 2009; FONTANILLES *et al.*, 2010; ARIZAGA *et al.*, 2011b; CHENAVAL *et al.*, 2011).

The sampling period lasted for 28 days, from 1<sup>st</sup> to August 28<sup>th</sup> 2011, coinciding with the main period of passage of Aquatic Warbler (ATIENZA *et al.*, 2001), and hence being the best period to sample possible stopping-over migrants. Birds were captured with mist nets (16mm-mesh, 5 shelves, 2.5 m-high) placed across the vegetation, always at the same site and time (a period of 4 h starting at dawn). Following JULLIARD *et al.* (2006), we used a tape lure of an Aquatic Warbler male's breeding song at all sites, placed every 36 meters of mist nets. The number of linear meters of mist nets differed between stations, although this variable was kept constant at each site (TAB. I). Daily sampling sessions were conducted at each site.

Reed beds were the only vegetation type common to all study sites and therefore, to preclude a possible bias on data interpretation associated to sampling habitats we only considered data obtained in reedbeds (TAB. I).

Captured birds were ringed and their age classified (following SVENSSON, 1996), either as first-year birds (hatched in 2011) or adults (older birds). We also recorded body mass ( $\pm 0.1$  g) and wing length ( $\pm 1$  mm; method III by SVENSSON, 1996) and then the birds were released.

| Site         | Code | Sampling effort [metres] | REED | HERB <sup>(1)</sup> | BUSH <sup>(2)</sup> | TREE <sup>(3)</sup> | FREE |
|--------------|------|--------------------------|------|---------------------|---------------------|---------------------|------|
| Loire        | DON  | 144                      | 0.95 | 0.05                | 0.00                | 0.00                | 0.00 |
| Gironde      | GIR  | 108                      | 1.00 | 0.00                | 0.00                | 0.00                | 0.00 |
| Adour        | VIE  | 216                      | 0.75 | 0.15                | 0.00                | 0.10                | 0.00 |
| Txingudi     | TXI  | 204                      | 0.80 | 0.15                | 0.00                | 0.00                | 0.05 |
| Urdaibai     | URD  | 144                      | 0.70 | 0.15                | 0.05                | 0.05                | 0.05 |
| Villaviciosa | VIA  | 204                      | 0.85 | 0.15                | 0.00                | 0.00                | 0.00 |

<sup>(1)</sup> Dominant genera: Loire, *Bolboschoenus* spp.; Gironde, *Bolboschoenus* spp.; Adour, *Carex* spp.; Txingudi, *Bolboschoenus* spp.; Urdaibai, *Juncus* spp.; Villaviciosa, *Bolboschoenus* spp.

<sup>(2)</sup> Dominant genera: Urdaibai, *Baccharis* spp.

<sup>(3)</sup> Dominant genera: Adour, *Salix* spp., *Acer negundo*; Urdaibai, *Tamarix* spp.

## Data analyses

With the aim of estimating the importance of a site for the Aquatic Warbler, we used the 93 *Acrola* index, which is calculated as:

$$(1) \text{93} \text{Acrola} = k \times (C_{\text{acrola}} / C_{\text{acrocephalus}}) \times 100$$

where,  $k$  is the number of sampling days (28 in this case)/93 (i.e., duration, in days, of Aquatic Warbler passage in autumn, from July 15th to October 15th), in our study the  $k$  is 0.30 for all sampling stations;  $C_{\text{acrola}}$  is the sum of all captures of Aquatic Warbler, and  $C_{\text{acrocephalus}}$  is the sum of captures of all *Acrocephalus* warblers, including the Aquatic Warbler. To evaluate which stations had more or less than an expected (assuming a constant proportion of Aquatic Warbler across stations as null hypothesis) number of captures of Aquatic Warbler, we conducted a G-test on captures of Aquatic Warbler in relation to captures of all *Acrocephalus* warblers at each site. When the standardised difference (residual) between the observed and expected values was higher than 3, that difference was considered to be significant (AGRESTI, 2002).

We also checked whether age ratios differed between stations by conducting a G-test on the number of captures of both adult and first-year birds at each sampling site, assuming a constant proportion between age classes and stations as the null hypothesis. Stations with < 10 captures were omitted from this analysis (i.e. stations from northern Iberia). We did not consider Aquatic Warblers of undetermined age in this analysis.

To determine potential variation of fuel load between marshes we considered only those birds whose body mass and wing length had been measured and whose age was determined (i.e. identified as either first-year birds or adults). Only stations with a sample size  $\geq 10$  captures (or recaptures, but only the first capture event for each bird was considered in this analysis.) were considered. In migration, most of the mass of a bird in excess of its lean body mass is normally due to fat accumulation (e.g., SALEWSKI *et al.*, 2009). To assess fuel load we considered an index of body mass in relation to body size, here assessed with wing length (GOSLER *et al.*, 1998). To test if fuel load differed between stations we conducted an ANOVA on body mass/wing length with site and age as factors.

Statistical analyses were conducted with SPSS 18.0. All means are given  $\pm$  SE.

## RESULTS

Overall, we captured 11679 passerines (TAB. II), of which 145 birds were Aquatic Warbler.

The standardized number of captured tended to decrease from North to South in France, and it was very low along the coast of northern Iberia (TAB. II). The percentage of captures of Aquatic Warbler in relation to all *Acrocephalus* was 1.5% but this mean differed between stations ( $\chi^2 = 68.552$ ;  $df = 5$ ;  $p < 0.001$ ). Both the Adour and Gironde showed the highest *Acrola* indices

**TAB. II.**—Number of captures of all passerines and the Aquatic Warbler in particular, in August 2011 (from 1<sup>st</sup> to 28<sup>th</sup>). The last column shows number of within-season recaptures at each site.

*Nombre de captures des passereaux et tout particulièrement celles du Phragmite aquatique, en août 2011 (du 1<sup>er</sup> au 28). La dernière colonne indique le nombre de contrôles obtenus dans chaque site.*

| Site | Passerines | Aquatic Warbler <sup>(1)</sup> | Aquatic Warbler <sup>(2)</sup> | Recaptures |
|------|------------|--------------------------------|--------------------------------|------------|
| DON  | 7608       | 73                             | 1.8                            | 1          |
| GIR  | 1476       | 38                             | 1.3                            | 2          |
| VIE  | 977        | 17                             | 0.3                            | 2          |
| TXI  | 443        | 2                              | < 0.1                          | 0          |
| URD  | 508        | 7                              | 0.2                            | 2          |
| VIA  | 667        | 8                              | 0.1                            | 1          |

<sup>(1)</sup>Absolute number of captures; <sup>(2)</sup>Standardised number of captures (number of captures/100m/d).



**TABLE III.**— Observed percentage of captures of Aquatic Warbler in relation to all the *Acrocephalus* warblers, and the standardised residual values of the observed percentage in relation to the expected one assuming no difference among sites. Absolute residual values  $> 3$  indicate a significant difference between the observed and the expected percentage. Additionally, the 93Acrola index is shown.

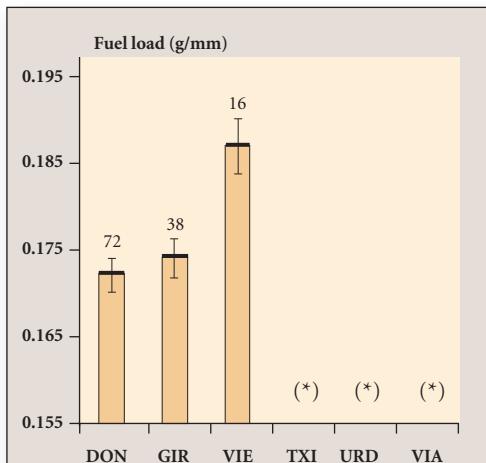
*Pourcentage des captures de Phragmite aquatique par rapport à tous les autres Acrocephalus et les valeurs résiduelles standardisées du pourcentage observé par rapport à celui attendu en supposant aucune différence entre les sites. Valeurs résiduelles absolues  $> 3$  indiquent une différence significative entre les valeurs observées et le pourcentage attendu. En outre, l'indice 93Acrola est signalé.*

|          | Percentage | Residual | 93Acrola |
|----------|------------|----------|----------|
| DON      | 1.0        | -3.3     | 0.30     |
| GIR      | 3.7        | +5.6     | 1.11     |
| VIE      | 4.2        | +4.3     | 1.26     |
| TXI      | 0.5        | -1.8     | 0.15     |
| URD      | 2.8        | +1.6     | 0.84     |
| VIA      | 2.1        | +0.9     | 0.63     |
| Expected | 1.5        |          |          |

**TABLE IV.**— Percentage of first-year birds (EURING code = 3) and standardised residual values of the observed percentage in relation to the expected one. Only the first capture event for each bird has been considered at each site. Stations from northern Iberia are not included due to their small sample size.

*Pourcentage des oiseaux de première année (code EURING = 3) et les valeurs résiduelles standardisées du pourcentage observé par rapport à celui attendu. Seul le premier événement de capture pour chaque oiseau a été examiné au niveau de chaque site. Les stations du Nord de l'Espagne ne sont pas incluses en raison de la faible grandeur de l'échantillon.*

|          | Percentage | Residual |
|----------|------------|----------|
| DON      | 82.2       | +0.7     |
| GIR      | 76.3       | +0.1     |
| VIE      | 41.2       | -1.6     |
| Expected | 75.0       |          |



**FIG. 2.**— Mean fuel load ( $\pm$  SE) for the Aquatic Warbler. The sample size was not sufficiently high ( $\geq 10$  captures) at the northern Iberian stations. The sample size of each site is shown above the bars.

*Réserve énergétique ( $\pm$  SE) moyenne pour le Phragmite aquatique. La taille de l'échantillon n'était pas suffisamment élevée ( $\geq 10$  captures) dans les stations ibériques du Nord. La grandeur de chaque site d'échantillonnage est indiquée au dessus des barres.*

(1.26% and 1.11%, respectively; Tab. III), without significant differences between these two sites, while one station (DON) showed less captures than expected (Acrola index: 0.30%; TAB. III).

Age ratios differed between stations [localities from northern Iberia not considered due to small sample sizes ( $\chi^2 = 12.421, df = 2; p = 0.001$ ; TAB. IV)]. The proportion of first-year birds tended to decrease from Loire to Adour (82.2% and 41.2%, respectively; TAB. IV).

Fuel load only differed between age classes (TAB. V). Overall, adults ( $0.186 \pm 0.003$  g/mm,  $n = 32$ ) were heavier than first-year birds ( $0.171 \pm 0.001$  g/mm,  $n = 94$ ). Fuel load at Adour tended to be higher than at the other two French sites located further North (FIG. 2), although the difference was not significant (TAB. V), partly due to the relatively small sample sizes. Wing length did not vary between sites (TAB. V). Aquatic Warblers were only recaptured on 8 occasions (TAB. II), so we were not able to assess if mass deposition rate differed between stations.

TABLE V.— ANOVA conducted to test if fuel load and wing length differed between stations. Fuel load was measured as a body mass/body size index.

*ANOVA a été effectuée pour vérifier si la réserve énergétique et la longueur des ailes étaient différentes entre les stations. La réserve énergétique a été mesurée par un indice de masse corporelle taille/corps.*

|             | SS      | df  | F      | p       |
|-------------|---------|-----|--------|---------|
| Fuel load   |         |     |        |         |
| Site        | 0.001   | 2   | 2.452  | 0.090   |
| Age         | 0.002   | 1   | 12.753 | 0.001   |
| Site × Age  | 0.000   | 2   | 0.831  | 0.438   |
| Error       | 0.023   | 120 |        |         |
| Wing length |         |     |        |         |
| Site        | 9.871   | 2   | 2.777  | 0.066   |
| Age         | 43.009  | 1   | 24.195 | < 0.001 |
| Site × Age  | 0.024   | 2   | 0.007  | 0.993   |
| Error       | 213.309 | 120 |        |         |

## DISCUSSION

The coast along the Bay of Biscay contains numerous wetlands that host several *Acrocephalus* species, including the threatened Aquatic Warbler. We observed that the Aquatic Warbler was more abundant (> 50% of captures) in northwestern France (Loire), decreasing from North to South along the coast of France and being rare along the coast of northern Iberia. However, when this abundance was expressed as a percentage over all the captures of *Acrocephalus* warblers (*Acrola* index), we observed that the Aquatic Warbler was proportionally more abundant in wetlands from southern France, without differences between them. Because this result was not due to a higher standardized number of captures at these last sites (FIG. 3), we link this difference to the fact that other *Acrocephalus* warblers, clearly Sedge Warbler *A. schoenobaenus*, were very abundant in northwestern France, confirming previous studies (CAILLAT *et al.*, 2005; CHENAVAL *et al.*, 2011). Therefore, it can be concluded that, (1) within the entire Bay of Biscay, the relevant stopover wetlands for the Aquatic Warbler are situated in northwestern France, with also some additional important (although less relevant) sites further south in France, but not in Iberia, and (2) the

*Acrola* index has clear interpretation biases because it is influenced by the relative abundance of the rest of *Acrocephalus* warblers. Regarding this last point it could be said that it is difficult to compare sites hosting different species, or populations, with different fuel requirements and migration strategies.

The wetlands along the coast of northern Iberia seem to play no more than a marginal role as potential stopovers, although in some circumstances (e.g. in case of adverse weather) the Aquatic Warbler may use these sites in northern Iberia as emergency stopovers (ARIZAGA *et al.*, 2011b). Under some conditions this temporal role can have a decisive impact for the conservation of a migrant species (OVERDIJK & NAVEDO, 2012). This result does not mean that all Iberia has a marginal role as a stopover region for the Aquatic Warbler: wetlands situated along the coast of Portugal have been reported to host good numbers of Aquatic Warbler (NETO *et al.*, 2010), as well as some inner wet areas (JUBETE, 2001).

The higher number of captures in northwest France may be due because the marshes there are large (> 2800 ha of reed beds), so they have a higher carrying capacity than other smaller marshes further south. However, the Gironde Estuary has an important extension of reed beds, so size of sites alone does not seem to be a sufficient reason for the high concentrations of Aquatic Warbler in northwestern France. Alternative causes explaining this phenomenon are: (1) that the species may experience a higher fuel deposition rate in northwestern France compared to sites located further South (JULLIARD *et al.*, 2006; ARIZAGA *et al.*, 2011a), so wetlands in this area could have been selected by the Aquatic Warbler as target fuelling places before the Sahara Desert crossing, as reported in other small trans-Saharan birds (BIBBY & GREEN, 1981). This is likely to have a direct link with the selection of migration routes/strategies. It is well known that the migratory direction has a clear genetic basis at least in passerines, probably also in many other bird species (BERTHOLD, 1996). Therefore, it is reasonable to consider that the Aquatic Warbler may have evolved to select migration routes allowing individual birds to stop

over in sites providing favorable conditions for migration and thus increasing individual fitness. Alternatively, (2) it could be stated that the particular geographic position of northwestern France promotes a possible funnel effect that would collect large numbers of birds moving along a north-south or south-west axis in their

route to southwestern Europe and Africa (BARGAIN *et al.*, 2002; WERNHAM *et al.*, 2002). Although this last hypothesis should be tested specifically, we consider it to be less likely than the first one, because the Aquatic Warbler is a scarce bird, coming from a relatively small breeding range from the East of Europe.

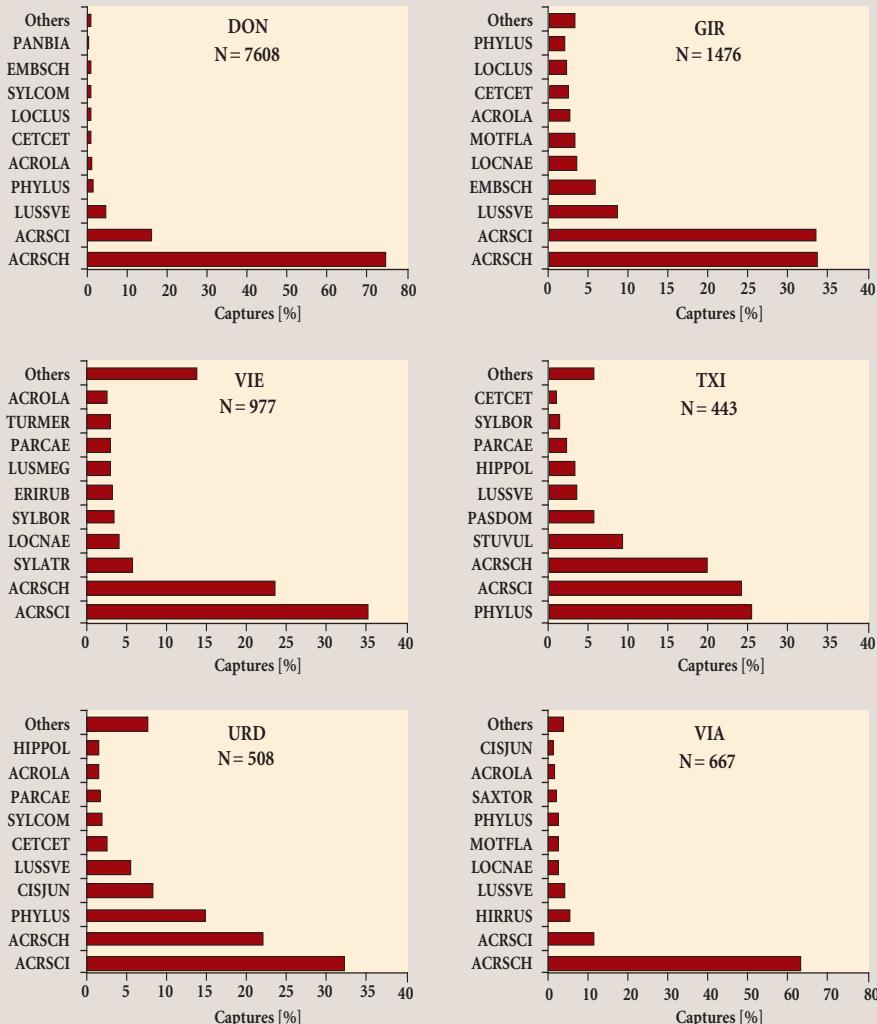


FIG. 3.—Abundance (as a percentage) of the ten most abundant passerines (each individual being considered only once at each site). Number of captures obtained at each site is also shown.

Abondance (en pourcentage) des dix passereaux les plus abondants (chacun étant considéré comme une seule fois sur chaque site). Le nombre de captures obtenues sur chaque site est également indiqué.

The proportion of first-year birds tended to decrease from North to South in France (analyses not done for Iberia). This result agrees with previous studies with similar warblers (BIBBY & GREEN, 1981). Causes explaining this pattern remain unknown to us, so we cannot do more than establish some plausible hypotheses. The higher-than-expected proportion of first-year birds in northern sites compared to southern ones may be due simply to the fact that the passage of adults is earlier than first-year birds (ATIENZA *et al.*, 2001). Thus, the species has been reported to pass over Iberia till the end of September (ATIENZA *et al.*, 2001), so an extended sampling period in Iberia could be useful to solve this question. Moreover, it is also possible that adults, with more experience, may take advantage from the several coastal marshes from southwestern France and to not depend so strongly on northwestern France, where they would meet more competition. We need detailed analyses on departure decisions in northwestern France to properly answer this question. First-year birds could also experience lower rates of fuel accumulation which would force them to migrate at lower speed, hence adults would be proportionally more abundant at southern localities. Finally (or complementarily), first-year birds could also experience lower survival rates which would result in a higher proportion of adults in more southern localities.

Fuel load tended to increase from North to South along the coast of France (analyses not done for Iberia due to the small sample sizes), although the difference was non-significant, likely due to the relatively small sample sizes. Our results would confirm a previous study where migrants caught in the Loire had the lightest fuel reserves (JULLIARD *et al.*, 2006). This does not mean that they experience lower fuelling rates in northwestern France but the result is consistent with the idea that birds from northwestern France constitute a mixture of newly arrived birds (with few fuel) and birds just about to depart (presumably with large fuel loads), whilst a high fraction of migrants captured in southwestern France could be birds just landed to rest but not to refuel consistently, since they would have sufficient fuel loads to reach Africa (JULLIARD *et al.*, 2006).

Again, as said for the discussion on ratios between age classes, we need detailed analyses on departure decisions in northwestern France as well as fuel deposition rates between first-years and adult birds to properly answer this question. Moreover, it is also noteworthy that our analyses involved birds captured in reedbeds but the Aquatic Warbler forages chiefly on low and wet vegetation (PROVOST *et al.*, 2010; MUSSEAU & HERRMANN, 2013), so it cannot be excluded that our results may have been different if they would have focused on this last habitat.

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