

Identifying autumn migration routes for the globally threatened Aquatic Warbler *Acrocephalus paludicola*

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The migration strategy of the globally threatened Aquatic Warbler *Acrocephalus paludicola* needs to be known to ensure that effective action is taken to conserve its principal stopover sites. Using data from ringing stations during the autumn migration of reedbed warblers, we developed an index that allowed countries and sites to be compared in terms of their numerical importance to migrating Aquatic Warblers. According to this index, there was no significant decline in the number of Aquatic Warblers migrating through Europe during the 1990s. France appears to receive the largest numbers of this species in autumn compared with other European countries. Within France, only coastal regions are visited by the species (but not in the Mediterranean), with the largest numbers occurring in Normandy and Loire, while Brittany receives large numbers in some years but not in others. We also identified some French sites that are of major importance to migrating Aquatic Warblers depositing reserves on migration. France therefore plays a very important part in providing stopover sites for Aquatic Warblers, which means that France should play a major role in undertaking conservation measures for this threatened species.

In order to migrate successfully, birds usually need to divide their migration into several flights separated by stopovers (Bairlein 1985, Biebach *et al.* 1986). The migration strategy of a species is defined by the succession of flights and stopovers as well as gains in body mass during stops (Ellegren 1991). Studying a stopover system within a country is a demanding task, but is achievable for some habitat-specialists such as reedbed passerines. Such species use wetland habitats, especially in coastal areas and estuaries, allowing the study of migrating individuals. Among reedbed warblers, the Aquatic Warbler *Acrocephalus paludicola* seems to make use of traditional stopover sites where many migrants gather (Atienza *et al.* 2001). Defining which potential stopover sites are important for this species (i.e. those that receive high numbers during migration) is therefore achievable by ringing at potential stopover sites along sea coasts.

The Aquatic Warbler is a globally threatened species (Collar *et al.* 1994), which occurs in western Europe as an uncommon but regular passage migrant, and is the focus of a European Action Plan (Heredia 1996). Breeding populations are reported to be declining

(Aquatic Warbler Conservation Team 1999, Kozulin & Flade 1999, Birdlife International 2004), mainly because of habitat loss (Dyrce & Zdunek 1993, Kozulin *et al.* 2004). This species is one of the most habitat-specialized reedbed warblers in Europe, inhabiting rich, flooded fen mires that are globally threatened by agriculture intensification and drainage. The species has now disappeared from its previous breeding grounds in France, Belgium, the Netherlands and Austria (Bargain 1999). In western Europe, its breeding range is now confined to Germany, with populations further east in Poland, Hungary, the Baltic States, Belarus, Ukraine and, to a lesser extent, Russia (5–50 pairs). Only 12–15 pairs breed in Germany and 250–310 pairs in Latvia and Lithuania, while the Hungarian population has recently risen to 350–700 pairs after the first breeding record in 1971 (Kovács & Végvári 1999, Birdlife International 2004). Poland (2700–2750 pairs), Belarus (6500–12 500 pairs) and Ukraine (2600–3400) constitute the breeding strongholds of the species (Heredia 1993, Kozulin & Flade 1999, Birdlife International 2004). The northern populations migrate westerly through western Europe during autumn, visiting marshes in the Netherlands, Belgium, France and the United Kingdom (de By 1990). The wintering grounds, somewhere in tropical Africa,

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have yet to be identified precisely. There are a few records from Senegal, Mali and Ghana (Heredia 1993). Stable isotope signatures from winter-grown feathers of different populations suggest a strong relationship between European breeding and African winter moulting latitudes, but did not help in localizing the wintering sites (Pain *et al.* 2004). For such a globally threatened passerine, identifying the system of stopover sites in each country crossed during migration is a high conservation priority. The stopover system of the Aquatic Warbler cannot be derived from what is known from congeners, as species of a genus can practise different migration strategies (Bibby & Green 1981), and as Aquatic Warblers breeding in Europe do indeed take a different, indirect, route for their post-nuptial migration from those taken by other *Acrocephalus* species (de By 1990, Sutherland 1998). Understanding the stopover sites system in Europe should allow us to define site-based conservation priorities to aid further in the conservation of the species.

The aims of the current study were three-fold. First, to use ringing data to describe any annual trend in the abundance of migrating Aquatic Warblers in France during the last decade, and to relate this to annual patterns observed in most European countries. The second objective was to define the importance of French stopover sites for migrating Aquatic Warblers, as compared with other European countries. The third objective was to study more precisely the system of stopover sites of the species at a regional level in France, during two years of intense and standardized monitoring (i.e. ringing) of potential stopover sites.

METHODS

Using ringing data to develop indices

We used data obtained from ringing programmes of reedbed warblers across various sites and countries, collected between 1990 and 2001. Yearly data from the different countries were provided by the corresponding national ringing centres. These countries are among those visited by the Aquatic Warbler during its post-nuptial migration, and are listed in Table 1 (from Poland and the Baltic States to Morocco). In each country, ringing was achieved by mist-netting without tape-luring, except at Tréogat/Baie d'Audierne in France and at some Spanish sites in 1999, 2000 and 2001. In France, yearly totals of ringed Aquatic Warblers varied from 51 to 166 for the period 1990–2001 (mean and median, 97).

Table 1. Values (\pm se) of mean Acrola index for countries considered in this study (period 1990–2001). The yearly Acrola index is defined as the proportion of Aquatic Warblers captured among all *Acrocephalus* warblers (as a percentage). The number of years for which data on ringed *Acrocephalus* warblers were available for calculating the index as well as the total number of Aquatic Warblers reported, in that order, are given in parentheses for each country.

Country	Acrola index
Poland (11; 1497)	2.286 \pm 1.834
France (12; 240)	0.184 \pm 0.097
Morocco (4; 3)	0.160 \pm 0.376
The Netherlands (9; 136)	0.079 \pm 0.026
Belgium (12; 476)	0.055 \pm 0.025
United Kingdom (11; 284)	0.049 \pm 0.030
Lithuania (12; 22)	0.048 \pm 0.125
Spain (9; 76)	0.047 \pm 0.044
Denmark (12; 8)	0.036 \pm 0.041
Germany and Austria (12; 60)	0.032 \pm 0.030
Switzerland (12; 4)	0.019 \pm 0.037
Italy (5; 4)	0.014 \pm 0.034
Sweden (12; 6)	0.003 \pm 0.003
Estonia (11; 1)	0.001 \pm 0.003

A second sampling method was used at Tréogat, France, from 1990 to 2003, and was extended to 28 other French sites in 2002 (Fig. 1) and nine sites in 2003. This method comprised tape-luring during capture sessions and a standardized spatial design of mist-nets. The latter were placed as mist-net lines perpendicular to the coast (most sites were next to the sea or large area of open water), with lines 50 m apart. The territorial song of Aquatic Warbler was played back at the centrally positioned mist-net line during the whole capture session, but never at night. Any day of capture started at dawn and stopped usually at noon, but most captures were concentrated in the first few hours.

In order to investigate annual, seasonal and spatial variations in Aquatic Warbler numbers, we developed an index, termed 'Acrola', defined as the total number of Aquatic Warblers captured divided by the total number of *Acrocephalus* warblers captured (as a percentage). This index allowed biases caused by heterogeneous capture effort between countries or sites to be accommodated. The rationale of such an index is that the actual spatial variation in Aquatic Warbler numbers is of greater magnitude than the variation in the total number of *Acrocephalus* warblers. This is probably because other *Acrocephalus* species come from very large populations (tens of millions of individuals), and at any location, populations from

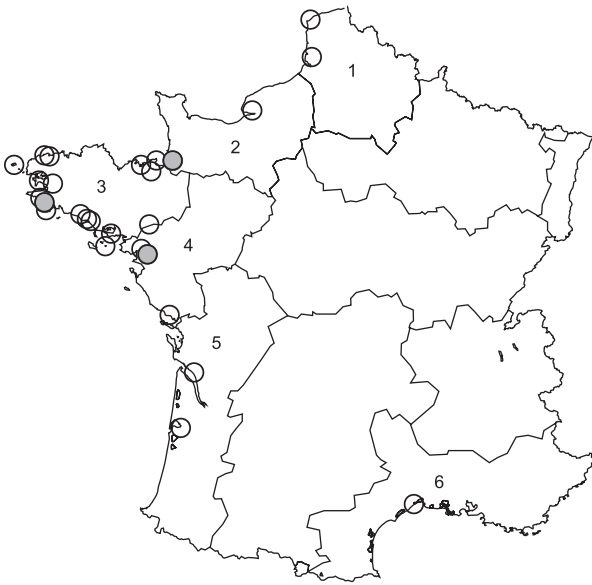


Figure 1. Location of French ringing sites (29) where a standardized mist-netting methodology (including tape-luring) was set up in July–September 2002 in order to capture migrating Aquatic Warblers. The three reference sites are represented by grey dots (from north to south: Genêts, Tréogat/Baie d'Audierne and Frossay). We defined ten regions grouping adjacent administrative regions on biogeographical criteria. Labels 1–6 refer to the regions listed in Table 2.

very large areas are mixing (from Ireland to Finland in various proportions). Hence, any potential stopover site receives a very large number of reedbed warblers, among which are a few Aquatic Warblers. Indeed, the Acrola index varies greatly, ranging from less than 0.01 to 1% (see Results). Such an order of magnitude cannot be due to variation in the number of *Acrocephalus* only. A second index was developed for French sites surveyed in 2002 and 2003 with the standardized methodology, as the mean number of Aquatic Warblers captured for 100 m of mist-nets and per day.

Comparing trends in indices between countries, 1990–2001

We first compared national indices obtained each year across various countries, excluding data obtained from sites using tape-luring in France and Spain (Table 1). Spatial and temporal variation in the Acrola index was modelled using standard General Linear Models for such data, assuming a binomial error distribution and using a logit link. In case of over-dispersion (residual deviance greater than residual

df), we used the *F*-statistic rather than the default chi-squared statistics. We looked for possible annual trends in this index over Europe from 1990 to 2001. The linear model considered effects of year (continuous) and country (factor). The presence of a non-linear trend was assessed with a non-parametric GAM model implemented in the S-plus software. We tested further whether trends obtained in France differed from those in other European countries (year \times country interaction in the linear model), and if the index was higher in France than in other European countries (ANOVA, country effect as France or non-France, after adjusting the index for any year effect).

Comparing indices between French sites, 1993–2001

We calculated the Acrola index for each year between 1993 and 2001 using ringing totals obtained in ten French administrative regions (see Fig. 1 for delimitation of these regions) and at two well-surveyed sites using tape-luring (Tréogat/Baie d'Audierne, Brittany, and Genêts, Manche, the latter for 1999–2001 only). We compared the index values obtained in these ten regions via an ANOVA (region effect adjusted to a year effect). We further compared annual trends in the index obtained at Tréogat (using tape-luring throughout the period) and at all other French sites (without tape-luring during the period).

Comparing indices between French sites, 2002 and 2003

In 2002, 29 French ringing sites used a standardized method to catch reedbed warblers, using tape-luring and a standardized spatial distribution of mist-nets. Three of these sites were almost constantly monitored during the post-nuptial migration period (from 15 July to 30 September). These are Tréogat/Baie d'Audierne (Brittany; 75 trapping days), Genêts (Normandy; 40 trapping days from 22 July to 15 September) and Frossay (Loire estuary; 83 trapping days), and are hereafter termed reference sites. Twenty-six additional sites were sampled during a shorter period within the post-nuptial migration (2–11 consecutive days for a total of 134 trapping days). Among-site variation in age ratio was examined by the use of a chi-squared test. In 2003, ten sites again employed the standardized method to catch Aquatic Warblers. In both years, the Acrola index was calculated for each site and for six regional areas. The latter are (names of corresponding administrative departments or regions in parentheses):

North (Nord, Pas de Calais; two sites in 2002, one site in 2003), Normandy (Basse and Haute Normandie; two sites in 2002 and 2003), Brittany (Bretagne; 17 sites in 2002, one in 2003), Loire (Loire-Atlantique, Vendée; five sites in 2002, four in 2003), Atlantic Coast (Charente-Maritime and Gironde; two sites in 2002 and 2003) and South (Hérault; one site in 2002).

Daily ringing records obtained in the three reference sites in 2002 were used to plot the daily captures of Aquatic Warblers in France during the post-nuptial migration period, from mid July to the end of September. We looked especially for seasonal trends in Aquatic Warblers caught in France during autumn 2002, to identify the peak migration period of the species in the country. We further compared the Acrola index values obtained in different sites or regions during the period identified as the migration peak. We also compared values of the second index we retained (number of Aquatic Warblers captured for 100 m of net per day) between sites and regions.

For 2003, we calculated the Acrola index for each site during the peak migration period before aggregating the indices to obtain a mean value for each of the six coastal regions.

Body mass: mean, variance and gain

Most birds captured in 2002 were weighed with a Pesola spring balance to the nearest 0.5 g. Variation in body mass was analysed with a standard ANOVA. The mean and variance of body mass were further

compared between the four main regions that had Aquatic Warblers. Variance was compared by use of the *F*-test (Snedecor & Cochran 1980). We estimated the body mass gain (in g/day) for individuals recaptured after one or more days using data for the period 1993–2002. We tested the linearity and non-linearity of the trend, for the 54 birds involved (using generalized linear and additive models).

All statistical analyses were performed using the S-PLUS package (MathSoft 1999). Results were considered significant at $P < 0.05$.

RESULTS

Comparing indices between countries, 1990–2001

We detected no significant annual linear trend in the Acrola index at a European scale from 1990 to 2001 ($F_{1,99} = 1.02$, $P > 0.3$; Fig. 2), when excluding data obtained in Poland (which includes birds ringed on breeding grounds) or obtained by tape-luring. We found no significant difference between linear trends obtained for France and for all other European countries when excluding Poland ($F_{1,98} = 0.98$, $P > 0.3$). Non-parametric GAM modelling did not detect any non-linear trend ($F_{3,96} = 0.68$, $P > 0.5$; Fig. 2). When comparing the Acrola index of France with those for all other countries combined, the French index appeared to be higher (Table 1; $F_{1,100} = 7.76$, $P = 0.006$). A negative linear trend obtained for Poland was only

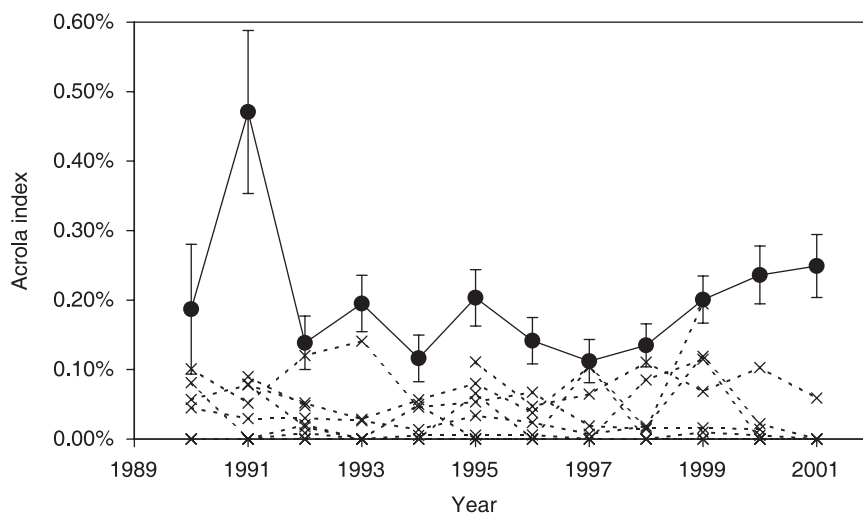


Figure 2. Annual variation of the Acrola index for 13 countries listed in Table 1 (period 1990–2001), excluding Poland where many ringed Aquatic Warblers are breeders, not migrants. Black dots, continuous line: France (vertical bars represent ± 1 se); crosses, dotted line: other countries.

weakly significant, but this differed from that obtained for all other European countries ($F_{1,109} = 4.02$, $P = 0.047$).

Comparing indices between French sites, 1993–2001

Tape-luring had a considerable effect on the Acrola index, which was thus increased approximately six-fold (Fig. 3). Among-year variations in the Acrola index were highly significant for Tréogat/Baie d'Audierne and all other sites (likelihood ratio test (LRT), $P < 0.001$), but were very similar between Tréogat/Baie d'Audierne and all other sites (same model, site \times year effect, χ^2 test, $P = 0.37$; correlation between yearly indices for Tréogat/Baie d'Audierne and all other sites, $r = 0.822$, $n = 9$, $P < 0.001$; Fig. 3). We found significant variation in the index across the ten regions ($F_{9,305} = 2.35$, $P = 0.014$), but no annual trend ($F_{1,306} = 2.18$, $P = 0.14$). The regions with the highest index values, in decreasing order, were: Atlantic Coast, Normandy and Brittany (Fig. 4).

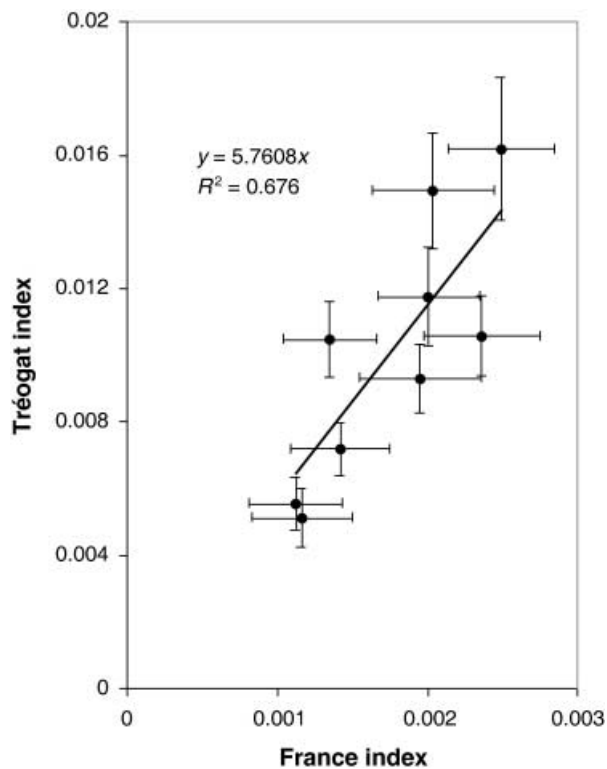


Figure 3. Comparisons of yearly Acrola indices obtained at Tréogat/Baie d'Audierne (using tape-luring) and all other French ringing sites (without tape-luring) for the period 1993–2001.

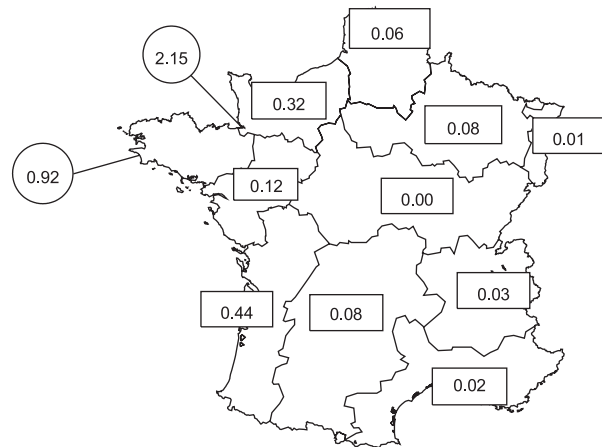


Figure 4. Variations in mean Acrola index across ten regions in France for the period 1993–2001. Two sites (circles) surveyed during the period using tape-luring are isolated in Normandy (Genêts) and Brittany (Tréogat/Baie d'Audierne).

Comparing French sites with a standardized method, 2002 and 2003

In total, 277 migrant Aquatic Warblers were caught in France in 2002. We found no significant difference in the distributions of juveniles and adults between the different sites (χ^2 test, $n = 274$ individuals, $P = 0.8$). We measured the numbers of Aquatic Warblers captured during days of migration for the three reference sites (Fig. 5). The migration peak of Aquatic Warblers in France could be derived from Figure 5 as occurring between 1 and 25 August. Within that period, the Acrola index showed no trend (LRT for a linear trend $\chi^2 = 0.12$, $df = 1$, $P = 0.7$; non-linear trend $\chi^2 = 4.12$, $df = 3$, $P = 0.19$). The Acrola indices were compared for the period 1–25 August only (Table 2). Frossay and Genêts were equivalent and seemed to be the most frequented sites, with an Acrola index four times greater than that for Tréogat/Baie d'Audierne in 2002. At a regional scale, Normandy and Loire were equivalent and seemed to be the most frequented regions, with an Acrola index three times greater than those for Brittany and the Atlantic Coast (Fig. 6).

Similarly, the number of Aquatic Warblers captured per 100 m of net per day was higher in Loire than in Normandy, Brittany or Atlantic Coast (Table 2). This index appeared to be successful in distinguishing between geographical areas and in distinguishing reference sites from each other. This index was twice as high at Frossay as at Genêts, with the latter's index

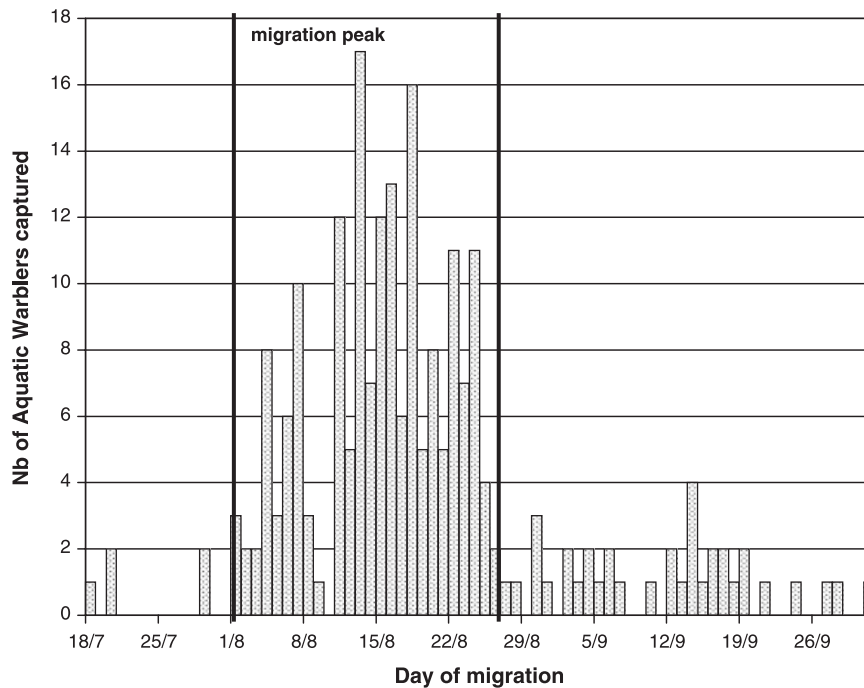


Figure 5. Daily numbers of Aquatic Warblers captured for three French reference sites (Tréogat/Baie d'Audierne, Genêts and Frossay), from 18 July to 30 September 2002.

Table 2. Values of two indices of Aquatic Warbler relative abundance for six regions (data obtained with a standardized mist-netting methodology; 1–25 August 2002). The respective indices are: the number of Aquatic Warblers captured for 100 m of mist-net per day, and the Acrola index. The mean body mass (in grams, \pm sd) and the variance of body mass of all captured Aquatic Warblers are also given, with the sample size considered (n). Regions are as shown on Figure 1.

Region (reference site)	No. of days of capture	No. of birds/100 m/day	Acrola index	Mean body mass	n
1. North	5	0.000	0.000	–	0
2. Normandy (Genêts)	23	0.965	3.395	11.51 \pm 0.99	40
3. Brittany (Tréogat)	53	0.402	1.064	11.20 \pm 1.14	52
4. Loire (Frossay)	36	2.139	3.539	10.92 \pm 0.79	151
5. Atlantic Coast	23	0.280	0.782	11.36 \pm 1.55	20
6. South	2	0.000	0.000	–	0

being also twice that at Tréogat/Baie d'Audierne (Table 2).

In total, 426 migrant Aquatic Warblers were caught in France in 2003. In that year, the index was three times higher in Brittany (Tréogat) than it had been in 2002 (Fig. 6). It was also higher than in 2002 for North and Atlantic Coast, almost similar to 2002 for Loire, but lower for Normandy. Overall, spatial variations of the index among regions were less marked than in 2002.

Body mass: mean, variance and gain

Body mass did not vary with date of capture (linear trend, $F_{1,257} = 0.13$, $P > 0.7$; non-linear trend estimated

with a GAM model, $F_{3,254} = 1.74$, $P = 0.16$). Adults tended to be slightly heavier than juveniles (adjusted to regional variation: $+0.44 \pm 0.23$ g (mean \pm sd); $P = 0.05$), such difference being additive over regions (age \times region, $F_{3,255} = 1.39$, $P = 0.25$). Average body mass varied strongly among regions ($F_{3,258} = 5.28$, $P = 0.001$; Table 2). Only birds from Loire differed significantly in body mass from those from other regions, those from Loire being lighter. We further calculated residual variance in body mass adjusted to age of the bird, and compared these variances among regions (Table 2). Birds captured in the Atlantic Coast region had higher variance in body mass than in Loire ($F_{17,147} = 4.16$, $P < 0.001$) and Normandy ($F_{17,37} = 2.52$, $P = 0.02$), but not Brittany ($F_{17,49} = 1.91$,

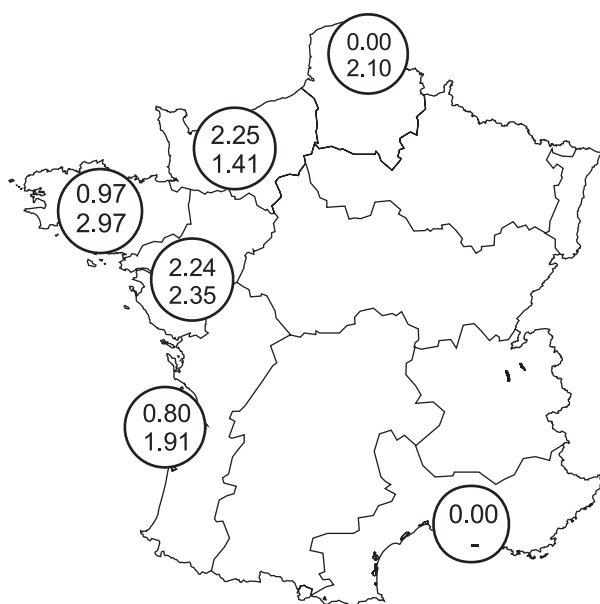


Figure 6. Variations in mean Acrola index across six regions in France in 2002 (top) and 2003 (bottom), for sites surveyed with a similar standardized mist-netting methodology and between 1 and 25 August.

$P > 0.05$). The only other significant difference was found between birds captured in Brittany and Loire, with a higher variance in body mass for the former ($F_{49,147} = 2.17$, $P < 0.001$).

We found a significant linear trend between body mass and time elapsed between two consecutive captures of the same individuals on a site ($F_{1,52} = 14.02$, $P < 0.001$), but no non-linear trend beyond (GAM modelling, $F_{3,52} = 1.97$, $P = 0.13$). The gain in mass was 0.29 g/day, and the intercept was not significantly different from zero ($t = -1.77$, $n = 52$, $P = 0.08$).

DISCUSSION

During the period 1991–2000, the breeding populations of the two most abundant *Acrocephalus* species (Sedge Warbler *A. schoenobaenus* and Reed Warbler *A. scirpaceus*) were increasing generally across Europe (Birdlife International 2004). This might have caused a negative bias in the Acrola index over time. The fact that we failed to detect any negative annual trend in relative numbers of Aquatic Warblers migrating across Europe and France is thus reliable. Yet numbers of breeding Aquatic Warblers have been reported to have decreased over the last decade at European breeding sites, especially because of habitat loss (Aquatic Warbler Conservation Team 1999, Birdlife Inter-

national 2004). Accordingly, we found a decreasing index for Poland over the last decade (including breeders and migrants), but this does not seem to have affected numbers migrating through western Europe. This could be corroborated by the recent re-estimation of numbers breeding in eastern European countries, which seem to be higher than previously suspected, and potentially exceeding the Polish populations (e.g. Kozulin & Flade 1999, Birdlife International 2004). The Aquatic Warbler may be declining in its westernmost breeding grounds, but not in the east, and its eastern breeding populations are larger than those in western Europe. With regard to the sampling methods used to capture migrating Aquatic Warblers, tape-luring did not influence the yearly index variations in France (Fig. 3). This provides further evidence that tape-luring is highly efficient for both capturing more Aquatic Warblers and increasing the accuracy in estimating annual trends in migrant numbers. It should be noted, however, that the Acrola index could be biased in some countries, which might receive proportionately more individuals of other *Acrocephalus* species. Using a second index, by quantifying the sampling effort differently, as the mean number of Aquatic Warblers captured per 100 m of net per day, should provide the opportunity to test this, although data on total mist-net lengths and duration of capture sessions are hardly accessible and rarely recorded by national ringing schemes.

In a European context, France appeared to receive the highest number of Aquatic Warblers during the post-nuptial migration period. The fact that the Acrola index varies along the presumed Aquatic Warbler flyway (from Poland to Spain) suggests that the Aquatic Warbler does not have the same strategy as other *Acrocephalus* species taken together. The species seems to fly quickly to France, where it concentrates: the index in northwest France is about four times greater than in neighbouring Belgium and the United Kingdom (Table 1, Fig. 4). Because the Acrola index is lower in southwest France and Spain, it is likely that part of the population departs directly from stopover sites in France to winter quarters in Africa without additional stops in Europe. In that respect, the Aquatic Warbler migration strategy appears to be closer to that of the Sedge Warbler than to that of the Reed Warbler. Sedge Warblers migrate earlier, and more rapidly, and most fly a long stage to West Africa from feeding grounds in northern France or southern England. By contrast, Reed Warblers migrate later, over a longer period and more slowly and split the journey by refuelling in Spain and Portugal

before the Mediterranean–Saharan crossing (Bibby & Green 1981). This is confirmed by the rate of weight gain of migrating Aquatic Warblers, as measured in France, which is close to that reported for the Sedge Warbler by Bibby and Green (1981). Atienza *et al.* (2001) published a synthesis of migration records of Aquatic Warbler in Spain, and suggested that the species has a Mediterranean route and an Atlantic route. However, the very low Acrola index value based on 1993–2001 data along the Mediterranean coast in France (Fig. 4) suggests that Aquatic Warblers seen in the Ebro valley and along the Spanish Mediterranean coast in autumn come from the Atlantic French coast. What proportion of the global Aquatic Warbler population make a true stopover there is certainly crucial for evaluating the relative importance of Spain in the stopover system of the species.

As France therefore plays a very important part in the stopover sites system of the Aquatic Warbler in Europe, it should play a major role in undertaking conservation measures for this threatened species. Within France, our study revealed that three regions hold especially high relative numbers of Aquatic Warblers. As expected, coastal areas accounted for the highest indices, but, within these areas, some hierarchical importance could be achieved by comparing indices. Large estuaries in Normandy and Pays-de-la-Loire largely contributed to elevating index values for these regions, a result supported by three different analyses, and based on two different indices: proportions of Aquatic Warblers captured among *Acrocephalus* warblers during 1993–2001 (without tape-luring), the same proportions during the 2002 ringing campaign with standardized mist-netting and tape-luring, and mean numbers of Aquatic Warblers captured for 100 m of mist-net per day, during the 2002 ringing campaign. Such concordant results validate, and give confidence in, the chosen approach to estimating and comparing the importance of stopover sites for migrating Aquatic Warblers.

Post-nuptial migration of Aquatic Warblers occurs during the whole summer in France, although it peaks during the third week of August, with the majority of birds present between 1 and 25 August. To compare the relative importance of French sites surveyed in 2002 and 2003, we therefore chose to restrict our calculation of the indices to this period. The resulting indices were highly concordant for two sites monitored with the standardized method over many years and proximate sites surveyed with the same method in 2002 (Acrola index values of 0.92 for Tréogat/

Baie d'Audierne during 1993–2001 and 0.97 for Brittany in 2002; 2.15 for Genêts during 1999–2001 and 2.25 for Normandy in 2002). Thus, the relative importance of at least these two regions does not seem to be affected greatly by among-year variations. Results obtained in 2003 differed from this general pattern. In that year, easterly winds predominated during August, and may have pushed a larger proportion of Aquatic Warblers migrating through France to stop at Tréogat/Baie d'Audierne, while numbers stopping at Genêts were lower than usual. The same situation may also have occurred in 1995, when the Acrola index for Tréogat/Baie d'Audierne rose to 3.30, the highest value ever recorded for this site during the period considered. In 2002, some sites with high index values also showed large variances in the body mass of captured Aquatic Warblers. If such a variance can be considered to indicate variable stages in body mass gain for individual birds, we could then predict these sites to be of greater importance for migrating Aquatic Warblers to store reserves during their migration. This is especially the case for small wetlands in Brittany and along the Atlantic coast. The Loire estuary, covered by very large areas of reedbeds, certainly receives large numbers of migrating Aquatic Warblers, although the birds probably do not stay in reedbeds after their arrival, probably dispersing to grasslands, and hence the high abundance indices but low mean and variance of body mass for birds captured there.

By measuring the relative importance of French coastal wetlands for migrating Aquatic Warblers, we can confidently identify three main regions as important for the conservation of this species, namely Normandy, the Atlantic Coast and Brittany. Accordingly, some wetland areas within these regions could be defined as priority sites: the Seine and Loire estuaries (very large wetlands), and smaller wetlands in Baie du Mont Saint-Michel (e.g. Genêts) and Brittany (e.g. Tréogat/Baie d'Audierne). The last of these regions further received higher relative numbers of migrating Aquatic Warblers under predominantly easterly winds during the migration peak, as occurred in 1995 and 2003. Having identified important stopover sites in France, further preservation and management of wetland habitats there might be crucial for the conservation of the threatened Aquatic Warbler. More research is needed to identify precisely the ecological needs of the species on stopover sites, to enable efficient habitat management measures to be defined and undertaken; hence, a LIFE (Financial Instrument for the Environment) programme is running in Brittany until 2008.

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REFERENCES

- Aquatic Warbler Conservation Team.** 1999. World population, trends and conservation status of the Aquatic Warbler *Acrocephalus paludicola*. *Vogelwelt* **120**: 65–85.
- Atienza, J.C., Pinilla, J. & Justribo, J.H.** 2001. Migration and conservation of the Aquatic Warbler *Acrocephalus paludicola* in Spain. *Ardeola* **48**: 197–208.
- Bairlein, F.** 1985. Body mass and fat deposition of Palearctic passerine migrants in the central Sahara. *Oecologia* **66**: 141–146.
- Bargain, B.** 1999. Phragmite aquatique *Acrocephalus paludicola*. In Rocamora, G. & Yeatman-Berthelot, D. (eds) *Oiseaux menacés et à surveiller en France. Listes rouges et recherche de priorités. Populations. Tendances. Menaces, Conservation*: 546–547. Paris: SEOF/LPO.
- Bibby, C.J. & Green, R.E.** 1981. Autumn migration strategies of Reed and Sedge Warblers. *Ornis Scand.* **12**: 1–12.
- Biebach, H., Friedrich, W. & Heine, G.** 1986. Interaction of body mass, fat, foraging and stopover period in trans-Saharan migrating passerine birds. *Oecologia* **69**: 370–379.
- Birdlife International.** 2004. *Birds in Europe. Populations, Estimates, Trends and Conservation Status*. Birdlife Conservation Series 12. Cambridge: Birdlife International.
- de By, R.A.** 1990. Migration of Aquatic Warbler in Western Europe. *Dutch Birding* **12**: 165–181.
- Collar, N.J., Crosby, M.J. & Stattersfield, A.J.** 1994. *Birds to Watch 2. The World List of Threatened Birds*. Birdlife Conservation Series 4. Cambridge: Birdlife International.
- Dyrce, A. & Zdunek, W.** 1993. Breeding statistics of the Aquatic Warbler *Acrocephalus paludicola* on the Biebrza marshes, northeast Poland. *J. Ornithol.* **134**: 317–323.
- Ellegren, H.** 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. *Ornis Scand.* **22**: 340–348.
- Heredia, B.** 1993. The status and conservation of Aquatic Warbler. *Birding World* **6**: 294–295.
- Heredia, B.** 1996. Action Plan for the Aquatic Warbler (*Acrocephalus paludicola*) in Europe. In Heredia, B., Rose, L. & Painter, M. (eds) *Globally Threatened Birds in Europe. Action Plans*: 327–338. Strasbourg: Council of Europe.
- Kovács, G. & Végvári, Z.** 1999. Population size and habitat of the Aquatic Warbler *Acrocephalus paludicola* in Hungary. *Vogelwelt* **120**: 121–126.
- Kozulin, A. & Flade, M.** 1999. Breeding habitat, abundance and conservation status of the Aquatic Warbler *Acrocephalus paludicola* in Belarus. *Vogelwelt* **120**: 97–111.
- Kozulin, A., Vergeichik, L. & Stepanovich, Y.** 2004. Factors affecting fluctuations of the Aquatic Warbler *Acrocephalus paludicola* population of Byelarusian mires. *Acta Ornithol.* **39**: 35–44.
- MathSoft, Inc.** 1999. *S-Plus 2000, Modern Statistics and Advanced Graphics*. Seattle: MathSoft, Data Analysis Products Division.
- Pain, D.J., Green, R.E., Giessing, B., Kozulin, A., Poluda, A., Ottosson, U., Flade, M. & Hilton, G.M.** 2004. Using stable isotopes to investigate migratory connectivity of the globally threatened Aquatic Warbler *Acrocephalus paludicola*. *Oecologia* **138**: 168–174.
- Snedecor, G.W. & Cochran, W.G.** 1980. *Statistical Methods*, 7th edn. Ames, Iowa: Iowa State University Press.
- Sutherland, W.J.** 1998. Evidence for flexibility and constraint in migration systems. *J. Avian Biol.* **29**: 441–446.

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