

Ecology of Aquatic Warblers *Acrocephalus paludicola* in a fall stopover area on the Atlantic coast of France

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Abstract. The Aquatic Warbler *Acrocephalus paludicola* is the only endangered songbird in continental Europe. This trans-Saharan migratory bird significantly transits along the French Atlantic coastline during post-breeding migration and the right bank of the Gironde estuary has been identified as an important stopover site. We studied the spatial occupancy strategies of stationing individuals during August of three successive years (2010–2012). We characterized habitat use by radio-tracking individuals revealing relatively small foraging ranges (6.6 ± 2.6 ha on average) with only 1 ha actually exploited (core area), and a relatively high habitat fragmentation rate. Capture-mark-recapture analyses assessed the average stopover duration of individuals and body-mass variations during their stopover. The estimated average stopover duration was 6.46 ± 0.46 days (95% confidence interval: 4.4–9.6). Lean birds tended to forage significantly more than stout birds: on average, they gain $2.81 \pm 0.89\%$ of their initial mass each day whereas stout birds only gain $0.12 \pm 0.56\%$. Analyses of droppings characterized the local diet. We noticed that Aquatic Warbler preferentially used partially-flooded or flooded habitats with heterogeneous and rather low vegetation, such as bulrush beds or bulrush beds mixed with reed beds. Orthoptera, Araneae and Hymenoptera represented the largest contributions to the consumed biomass (64.7%, 13.4% and 8.9% respectively). The importance of the fuel deposition rate of lean birds reflects the importance of the estuary as a stopover site for the species. It means that the available resources allow birds to replenish and continue their migration route. However, the sustainability of the site's functionality is questioned because of the evolution of habitats (erosion, rise in water levels and changes in food web).

Key words: stopover duration, diet, habitats, fuel deposition rate, post-breeding migration, radio tracking

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INTRODUCTION

Migratory birds spend a quarter of the year on migration (Zduniak & Yosef 2012) and their survival outside the breeding season clearly impacts the breeding number (Newton 2006). Thus it is important to identify and preserve the resources available on stopover sites, especially that birds spend more time on stopover sites than on flight (Zduniak & Yosef 2012). In these areas individuals can rest, wait for better weather conditions to continue their route, and replenish their energetic resources (Sutherland 1998). The conservation of migratory species involves the identification of

stopover sites and dedicated habitat management in order to maintain suitable resources that individuals can exploit (Sutherland 1998, Chernetsov 2006).

The Aquatic Warbler *Acrocephalus paludicola* is a trans-Saharan migratory songbird, abundant in Europe until the 20th century when it started to become scarce due to habitat perturbations (essentially anthropogenic) on key breeding sites (De By 1990, Flade & Lachmann 2008, Tanneberger et al. 2008). Nowadays, the species breeds only in six European countries (Belarus, Germany, Hungary, Lithuania, Poland and Ukraine) and on only 40 sites covering a total

around 1,000 km² (Flade & Lachmann 2008). Almost 80% of the breeding population is concentrated at four sites in Belarus, Ukraine and Poland (Flade & Lachmann 2008). With a population size estimated between 11,000 and 16,000 singing males (BirdLife International 2012), the Aquatic Warbler is the only threatened passerine for continental Europe. The species is red-listed as “vulnerable” by the IUCN (BirdLife International 2004).

France is one of the European countries hosting the most important number of migrant Aquatic Warbler during post breeding migration (between 24,000 and 30,000 individuals; Jiguet et al. 2011). For France, the development of studies and management measures on key stopover sites is fundamental for its global conservation. In the Charente-Maritime, the right bank of the Gironde estuary is one of the most important stopover areas for the Aquatic Warbler within the country (Le Nevé et al. 2013, Musseau & Herrmann 2013). Nevertheless, erosion and siltation phenomena induce vegetation changes on the site. In the context of political obligation to implement conservation measures to ensure a favorable conservation status for the Aquatic Warbler, we implemented a field survey aiming at characterizing stopover strategies of the species during the post-breeding migration in the Gironde estuary over three years (2010–2012), to (1) characterize the habitats used by migrants along sub-halophic shore meadows (an original stopover site in France where Aquatic Warblers mainly stop in coastal marshes); (2) estimate the stopover duration with a capture-mark-recapture framework; (3) study the fuel deposition rate of birds to inform on stopover quality for refueling. Finally, we characterized the species diet in the Gironde estuary by analyzing droppings collected during the ringing sessions (see Kerbiriou et al. 2011) before discussing the necessity to organize habitat conservation and management at such stopover sites to ensure its suitability as an efficient refueling site for migrant Aquatic Warblers. Our study presents some redundancies with other works but studies on stopover sites used by the Aquatic Warbler are needed to clarify its migration and its refueling strategies (Schaub & Jenni 2001, Neto et al. 2010). Furthermore, reproducibility of scientific research is critical to the scientific endeavour and the apparent lack of reproducibility threatens the credibility of the scientific enterprise. Unfortunately, concern over the non-reproducibility of scientific studies has become pervasive (Johnson 2013). In the particular case of threatened species, when conservation

management actions have to be planned, managers need robust evidence, and so we therefore need to replicate studies in different sites with the aim of evaluating the generality of preliminary results. Judging by the level of threats to Aquatic Warbler populations, this study provides complementary elements which are indispensable for efficient site managements throughout the entire length of the migratory routes of this species.

MATERIALS AND METHODS

Study site

We conducted our survey at Conchemarche (France, 45°28'44"N, 0°49'06"W), a 250-ha area along the right bank of the Gironde estuary. The site is owned by the Conservatoire du Littoral and managed by the Conservatoire d'Espaces Naturels of Poitou-Charentes. Located between two municipalities of the department of the Charente-Maritime (Chenac-Saint-Seurin-d'Uzet and Mortagne-sur-Gironde), the site hosts numerous Aquatic Warblers during the post-breeding migration (Musseau & Herrmann 2013). The site is essentially composed of two distinct habitats. The first, along the estuary, is a *schorre* with huge dense sub-halophilic meadows with *Elymus pycnanthus* and almost monospecific reed beds with *Phragmites australis*. The second, behind the first, covering about 190-ha, is a former agricultural polder which has evolved in a laguna under tidal influence since the Lothar and Martin storms of December 1999 (Hérault & Collet 2010). In the latter a bulrush bed mixed with reed bed (zone dominated vegetation by *Bolboschoenus (Scirpus) maritimus* and *Phragmites australis*) develops with a very heterogeneous structure and evolves with siltation and erosion phenomena. These two areas are located in the heart of a linear eco-complex subject to tides. This eco-complex covers an area around 1,300 hectares of more than 20 kilometers in length and from one hundred meters to more than one kilometer in width. This habitat is composed of sub-halophilic meadows, reed beds and numerous flooded depressions created for waterfowl hunting.

Capture and ringing

Catches of birds were conducted between the 1st to the 31st of August of each monitoring year. In 2010, birds were captured with a straight line of 9 mist nets (12 m × 2.50 m, 16 mm mesh, 5 shelves). This 108-meter-long line was at the heart of a

dense and homogeneous reed bed of the intertidal zone of the estuary. The protocol implemented was the "ACROLA" protocol developed by the National Museum of Natural History (Jiguet et al. 2012). Nets were opened for 5 hours every morning from one hour before the official time of sunrise. At the centre of each sub-unit of three nets a tape lure (playback) broadcasting the Aquatic Warbler's song started 1.5 hours before sunrise and stopped at the time of closing the nets. As the Aquatic Warbler migrates at night, no night playback is allowed to avoid modifying the stopover strategy of the species. After capture, birds were identified (species, age and sex) according to the criteria detailed by Svensson (1996) and ringed. All birds were weighed with an electronic balance (capacity: 120 g, readability: ± 0.1 g) each time they were captured and their wings were measured using the flattened straightened method (Svensson 1996) with a stopped rule to the nearest 0.5 mm. In 2011 and 2012 a similar protocol was set up, but to maximize the number of captures, and to compare their distribution between different habitats, the number of nets was doubled (18 mist nets) and distributed through two habitats of the study area. Half of the nets were again installed in homogeneous reed beds of the shore (as in 2010) while the other half were placed in a bulrush-reed bed of the laguna. During these two years, to increase the recapture probabilities of marked birds, the 18 mist nets were arranged in units of three nets distributed in space to cover larger areas and with different orientations. A similar arrangement has been used in both habitats (Fig. 1). Estimates of stopover duration were obtained with data collected with this last configuration. The protocol established in 2010 is presented above to detail the conditions under which radio-tracked birds were captured in 2010.

Radio tracking

In 2010 and 2011, we fitted a total of 20 Aquatic Warblers (10 birds per year, young and adults) with radio transmitters. We used "pip" (0.45 grams) and "pico-pip" (0.35 grams) tags from Biotrack (Ltd.). These tags were chosen in order not to exceed 5% of the body mass of individuals (fixing kit included). The average detection range of these transmitters was 80–300 meters. Tags were configured to radiate in the 148 MHz frequency range with the emission of one signal per second (20 milliseconds pulse length). To avoid tags remaining for too long a period on birds, and not to penalize animals during their further migration

route, we chose to glue transmitters on the back of birds to expect tags to fall within a maximum period of about ten days. For this we stuck transmitters on a piece of surgical gauze and this set was placed on the back feathers of birds under which a thin and narrow strip of adhesive tape was positioned to protect the skin of animals from possible contact with the glue. These collages were done with cyanoacrylate Loctite 401 TM glue. Tagged birds were released at the place of their capture. Once released, the location of the birds was performed using a directional Yagi-Uda antenna and a Sika (Biotrack Ltd.) receiver. At every contact with a transmitter, the geographical coordinates of the contact point were recorded on a GPS and signal direction relative to magnetic north (azimuth) was determined using the directional antenna and a magnetic compass. From a minimum of three geo-referenced locations and azimuths associated with these points, locations of the birds were determined according to the principle of triangulation defined by White & Garrott (1990). The fieldwork was conducted in order to obtain, to the extent possible, one location every 15 minutes for each monitored bird. This work was conducted daily for six hours starting one hour before the official time of sunrise.

Dropping gathering and prey identification

The diet of the Aquatic Warbler was assessed by analyzing droppings. In order to collect these droppings the captured birds were placed for a few minutes (during the walk from the mist net to the ringing station) in cloth bags equipped with a plastic bag at the bottom, just before being ringed and released. Droppings were individually stored in small tubes with 70% alcohol. They were further dissected under a binocular microscope. Identifiable chitinous fragments were counted in each sample with the aim of estimating the minimum number of individuals of each taxonomic group (e.g. four Hymenoptera wings were counted as one individual). This method is likely to lead to some bias in diet evaluation because small or soft-bodied prey items are less easily detected. However, Davies (1977a,b) demonstrated that there is a strong correlation between prey remaining in droppings and the composition of the true diet in other insectivorous passerines. In addition to the number of prey per dropping and to the occurrence of prey, we assessed prey biomass using a predictive model based on the relationship between the body length of the concerned invertebrate groups and their mass (Ganihar 1997).

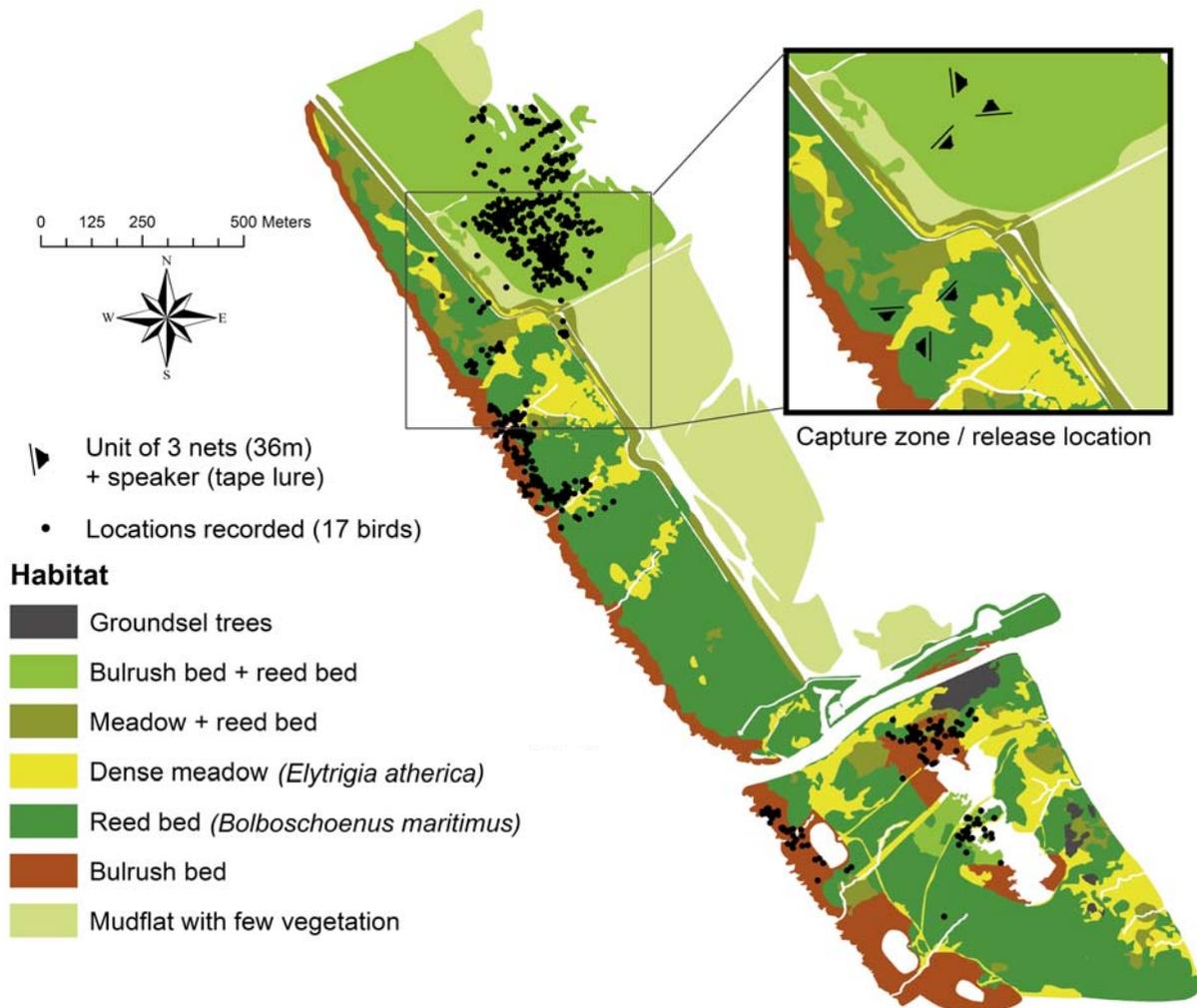


Fig. 1. Mistnet arrangement at Conchemarche site used during August 2011 and 2012 to study stopover duration of the Aquatic Warbler and locations of the 17 radio-tracked birds.

STATISTICAL ANALYSIS

Habitat use

Locations recorded the day of tag fitting were removed from the analysis to avoid potential behavioral biases that may be related to the stress of capture or an adjustment period inherent to the radio tag equipment. Ranges explored by monitored birds were estimated by calculating Minimum Convex Polygons (MCP, described by Mohr 1947 and discussed by Harris et al. 1990). MCPs are polygons that pass through the outlier points of a set of locations. Their angles are less than 180° . The distribution of locations in the MCP being not necessarily homogeneous, it is important to identify areas with high occupancy (high density of locations) called core areas, which correspond to the areas actually exploited by birds.

These areas were calculated with the "cluster convex polygons" method (Kenward 1987, Kenward et al. 2001), excluding the outliers locations in the largest 5% of the nearest-neighbour distance distribution ("objective cores" method, Hodder et al. 1998, Kenward et al. 2001). Eventually, the fragmentation of these ranges, called "partial areas" (C_{part} , Hodder et al. 1998, Walls et al. 1999), were evaluated by the ratio of the separated core areas and the area of the single polygon including all "core areas". This index ranges from 0 to 1. A value close to 0 indicates a high level of fragmentation of the space used by individuals, while a value close to 1 indicates that birds exploited a single continuous area. All these analyses were performed using Ranges 8 v.2.9 (Anatrack Ltd.; Kenward et al. 2008). These area calculations were performed with individuals for whom we have

observed at least one flattening of the curve representing the evolution of the explored area versus the addition of locations.

For all recorded locations, we sought to determine whether they were randomly distributed over space or if their distribution mirrored a preference for some habitats. To do this, under ArcGIS software, a grid layer (100 × 100 m) was superimposed onto a map of the study area covering all recorded positions where birds had been recorded. Grid cells constituted of only open water or mudflat were excluded. In each remaining grid cell the number of locations was recorded. We then noted K_{noobs} , the observed number of grid cells containing n locations. The obtained K_{noobs} distribution was compared to a theoretical random distribution with a Chi-square test ($\alpha = 5\%$). This theoretical distribution is the distribution of K_{nth} (theoretical numbers of grid cells with n locations), calculated by $K_{\text{nth}} = [K^*(D^n/n!)]*\exp(-D)$ where K is the total number of grid cells, n the considered number of locations for each K_{nth} , and D the average density of locations by cell calculated by the K/N , N being the total number of locations.

The most frequented habitats were identified using the electivity index of Jacobs (Jacobs 1974). This is a selection/rejection index of habitats accounting for the availability of habitats. The Jacobs index is calculated as follows: $D = (r-p)/(r+p-2rp)$ where r is the proportion of locations in the habitat and p the proportion of the same habitat in the study area. Here the study area is the total surface of the MCP measured with all the locations without distinction of individuals. We used the proportion of locations instead of the proportion of areas in core areas to account for the edge effect (this avoids having, for instance, a core area with almost 100% of reed bed while the bird used only habitats at the edge of the reed bed). We also decided to compare only two groups of habitats: habitats hugely influenced by the presence of water (flooded or subject to tides: bulrush bed and bulrush bed mixed with reed bed), and habitats much less linked to water, homogeneous and dense (reed bed, meadows, reed bed mixed with meadows, Groundsel Bushes *Baccharis halimifolia*, see Fig. 1). The index ranges between -1 (rejection) and 1 (selection).

Stopover duration

As age ratio was highly biased among capture, 82.55% of birds were juveniles (78.02% in 2011 and 88.39% in 2012), we focused on the stopover dura-

tion of young birds. The average stopover duration (S_i) was estimated by adding the average stopover duration after capture (S_a) and the average stopover duration before capture (S_b). The values of S_a and S_b were calculated with equations proposed by Schaub et al. (2001), with $S_a = -1/\ln\varphi$ and $S_b = -1/\ln\gamma$, where φ (survival) is defined as the average probability that an individual present at the time i was still in the population at time $i+1$, and γ (seniority) is defined as the average probability that an individual present in the population at time i was already in the population at time $i-1$. The probability of survival was estimated using the Cormack-Jolly-Seber (CJS) model detailed by Lebreton et al. (1992), while the seniority was estimated using the Pradel model (Pradel 1996). Calculations were performed from models implemented in Mark software (White & Burnham 1999). To estimate survival probabilities and seniority we tested 5 possibilities: identical probabilities for the two years and for all days in August (φ_{cst} and γ_{cst}); identical probabilities for the two years but varying between days (φ_t and γ_t); probabilities different from one year to the other but constant throughout days (φ_{year} and γ_{year}); probabilities different from one year to the other and varying between days in the same way for two years ($\varphi_{\text{year}+t}$ and $\gamma_{\text{year}+t}$); and, finally, probabilities different from one year to the other and varying between days differently for the two years (φ_{year^*t} and γ_{year^*t}). These five options were also tested to estimate the average probability p_r that individuals captured at time i are recaptured at time $i+1$ for the CJS model, and the average probability p_c that individuals captured at time i have been captured at time $i-1$ for the Pradel model. In total, for the estimation of survival (φ) and seniority (γ), 25 models (five possibilities for φ and for γ , combined with five possibilities for the probabilities p_r and p_c) were tested. The selection of the most plausible models was based on the corrected Akaike Information Criterion (AICc, Burnham & Anderson 2002). If the difference in AICc between two models was less than 2, the model selected was the most parsimonious (Lebreton et al. 1992). Before running these models, the fit of the data to the CJS model (transience test and trap-dependence test) was tested using U-CARE software (Goodness Of Fit test, GOF test, Choquet et al. 2009).

Fuel deposition

Because adults and young do not have the same foraging skills and nutrient assimilations (Woodrey

2000), we analyzed Relative Fuel Deposition (RFD) only on yearling birds, representing the largest number of captures. We excluded birds that have been recaptured only once on the day after their initial capture because handling at first capture may have a negative effect on the body-mass within the day of capture (Schwilch & Jenni 2001). Thus, only birds having been recaptured at least one time and at least after 48 ± 5 hours after initial capture are considered in our analysis. Given radio-tags can influence birds' behaviour, no radio-tagged birds had been taken into account for the analysis (only one bird concerned in our data set). The RFD was calculated as: $RFD = (M_f - M_i) / M_i$, where M_f is the body mass measured at the final recapture and M_i is the body mass measured at the initial capture. We used a generalized linear model (GLM) to test whether RFD was affected by the individual Minimum Length Stopover (MLS) or by the Initial Body Mass Index (IBMI). The MLS had been measured for each bird by the difference in days between its initial date of capture and its final date of recapture. As wing length is a good proxy for body size (Pearson 1971), we calculated the IBMI as the ratio between M_i and wing length (Safriel & Lavee 1988). In order to cure heteroscedasticity in GLM analysis, we log-transformed M_i and M_f . The IBMI of the population sampled followed a normal distribution (Shapiro-Wilk normality test: $W = 0.971$, $p = 0.74$). To test whether Relative Fuel Deposition (RFD) was affected by the individual Minimum Length Stopover (MLS) or by the Initial Body Mass Index (IBMI), we ran a GLM fitted with a gaussian error distribution with an identity link. The model was correctly fitted to the Gaussian distribution: residuals normally distributed (Shapiro-Wilk normality test, $W = 0.937$, $p = 0.17$), homoscedasticity (studentized Breusch-Pagan test, $BP = 0.590$, $df = 2$, $p = 0.74$), and residuals not autocorrelated (Durbin-Watson test, $DW = 2.757$, $p = 0.93$). A type-II analysis-of-variance (Shaw & Mitchell-Olds 1933) was used to test the significance level of those potential effects of the explanatory variables. All statistical analyses were performed using the R software (R Development Core Team 2013).

Diet study

With the aim of evaluating sample size representativeness, we used species accumulation curves (R package *vegan*, function "specaccum"; Jari et al. 2013) which allowed assessing the expected mean species richness for a certain number of sampled

sites. We used a Generalized Linear Model (GLM) to look for potential variations of different prey abundances between years and between age classes (first-year and adults). Effects of these two explanatory variables were tested using a type-II analysis-of-variance (Shaw & Mitchell-Olds 1933). According to the nature of the data (counts) we used a Poisson error distribution with a log link (Crawley 2009) to run models. P-values were corrected for over-dispersion according to Faraway (2006). GLM and ANOVA were performed using the R software (R Development Core Team 2013).

RESULTS

Habitat use

In total, among the 20 birds tagged with a radio transmitter, 17 were successfully monitored (13 young and 4 adults). The sampled population was not large enough to consider testing validly a possible age effect on habitat use. The mean duration of monitoring for one individual was 3.35 ± 0.57 days (excluding the first monitoring day). A total of 926 locations (distributed over an area of 121.21 ha) were recorded. The maximum distance observed from the release location was 1 940 m. The comparison of the observed distribution of locations was significantly different from a random distribution ($\chi^2 = 12818.26$, $df = 9$, $p < 0.005$). This means that individuals do not randomly use the available habitats. The Jacobs index revealed that heterogeneous vegetation flooded or submitted to tidal influence was preferentially selected by the monitored birds ($D = 0.41 \pm 0.19$), while more dense and less wet habitats had a negative index. These radio-tracking results were confirmed by the ratio between captures in dry pure reed bed and in bulrush bed mixed with reed bed submitted to tidal influence. In total, $77.8 \pm 0.02\%$ ($79.12 \pm 0.03\%$ in 2011 and $76.26 \pm 0.04\%$ in 2012) of the first capture events of individuals occurred in bulrush bed mixed with reed bed. Among the 17 individuals monitored, 14 (11 young and 3 adults) showed at least one flattening on the curve representing the evolution of the explored area versus the addition of locations. On this sample, the average MCP was 6.64 ± 2.64 ha. The average area actually exploited (core areas) was 1.00 ± 0.21 ha. The average ratio between individual core areas and the polygon containing all core areas (C_{part}) was 0.32 ± 0.06 , which means a relatively high fragmentation of the used area.

Stopover duration

Analyses included 265 young birds (142 individuals captured in August 2011 and 123 captured in August 2012). The average recapture rate was $12.45 \pm 0.20\%$ ($11.97 \pm 0.27\%$ in 2011 vs. $13.01 \pm 0.30\%$ in 2012). Based on the AICc and the principle of parsimony, the selected models to estimate φ and γ were respectively $\{\varphi, p_r\}$ (Table 1) and $\{\gamma, p_c\}$ (Table 2). The selected models indicated the probability that an individual captured at time i remained in the population at time $i+1$, and the probability that an individual captured at time i was already in the population at time $i-1$ are constant among days and years, as were the probabilities to be recaptured at time $i+1$ or having been captured at time $i-1$. For these models, we obtained $\varphi = 0.74 \pm 0.05$ (0.64–0.82 in the 95% confidence interval, 95% CI) and $\gamma = 0.73 \pm 0.04$ (95% CI, 0.63–0.80). A model averaging was run for the estimation of γ (delta AICc was less than 2 for the second and third models) but since results were very close (0.72 ± 0.05 in 2011 and 0.73 ± 0.05 in 2012) we kept the first model's estimates. These results allowed us to calculate the stopover duration of birds after capture $S_a = 3.34 \pm 0.32$ days (95% CI, 2.26–5.05) and the stopover duration before capture $S_b = 3.12 \pm 0.32$ days (95% CI, 2.18–4.56). Thus the estimated average global stopover duration of individuals in the study area was $S_i = 6.46 \pm 0.46$ (4.44–9.61 in the 95% CI) days.

Fuel deposition

The fuel deposition analysis concerned 22 first-year birds. The average RFD was 0.03 ± 0.02 . The average MLS was 3.95 ± 0.45 days and the average IBMI was 0.17 ± 0.003 . A Spearman Rank correlation test revealed that explanatory variables IBMI and MLS were not correlated ($S = 1061.82$, $p = 0.06$, $\rho = 0.40$). Model results indicated that the RFD was not influenced by the MLS

Table 1. Five best models tested to obtain estimates of the mean survival rate of ringed Aquatic Warblers during their stopover at the Gironde estuary (the selected model appears in bold). φ — survival, p_r — capture probability. Notation for effects: t — time (days of August), . — constant, $year$ — year (2011 or 2012).

Model	AICc	Delta AICc	AICc weight	No. of parameters
φ, p_r	334.88	0.00	0.54	2
$\varphi_{year} p_r$	336.92	2.04	0.19	3
$\varphi, p_r year$	336.92	2.04	0.19	3
$\varphi_{year} p_r year$	338.97	4.09	0.07	4
$\varphi, p_r t$	381.66	46.80	0.00	31

Table 2. Five best models tested to obtain estimates of the mean seniority rate of ringed Aquatic Warblers during their stopover at the Gironde estuary (the selected model appears in bold). γ — seniority; p_c — capture probability. Notation for effects: t — time (days of August), . — constant; $year$ — year (2011 or 2012).

Model	AICc	Delta AICc	AICc weight	No. of parameters
γ, p_c	337.94	0.00	0.51	2
$\gamma_{year} p_c$	339.65	1.71	0.22	3
$\gamma, p_c year$	339.87	1.93	0.19	3
$\gamma_{year} p_c year$	341.69	3.75	0.08	4
$\gamma, p_c t$	363.47	25.53	0.00	31

($F_{1,19} = 1.85$, $p = 0.19$), while it was significantly and negatively influenced by the IBMI. This means that birds with a low IBMI tended to accumulate more mass than birds with high IBMI (Fig. 2, $F_{1,19} = 5.65$, $p = 0.03$, $\beta = -1.21 \pm 0.51$). On average birds accumulated $1.46 \pm 0.59\%$ of their initial mass every day (Daily Fuel Deposition Rate: DFDR, calculated as $DFDR = RFD/MLS \times 100$). Illustrating food availability, the fuel deposition could be considered as a fairly good indicator of the quality of the habitats (Cohen et al. 2014). Nevertheless, given the RFD was significantly affected by the IBMI, the DFDR average value obtained must be considered with caution because an average value can mask possible different foraging and fuel deposition strategies depending on the body conditions of birds. We then tested how the DFDR tended to change depending on the IBMI. For this, we used the IBMI median value (0.17) to separate birds into two groups: “lean birds” (with an IBMI < 0.17) and “stout birds” (with an IBMI > 0.17). The analysis revealed a significant difference between the DFDR of stout birds (accumulating only $0.12 \pm 0.56\%$ of their initial body mass every day) and the DFDR of lean birds (accumulating $2.81 \pm 0.89\%$ of their initial body mass every day, i.e. 23.43 times more than stout birds) (Mann-Whitney-Wilcoxon test, $W = 90$, $p = 0.01$).

Diet study

In August 2011 and 2012 we collected 26 and 77 droppings during ringing operations. Among those 103 samples, 17 belonged to adults (4 in 2011 and 13 in 2012). In total we identified 213 preys. On average each dropping contained 2.1 preys. The use of a rarefaction curve showed that from nine samples each additional sample provided less than 5% of new taxa. In terms of prey abundance the diet was dominated by Hemiptera

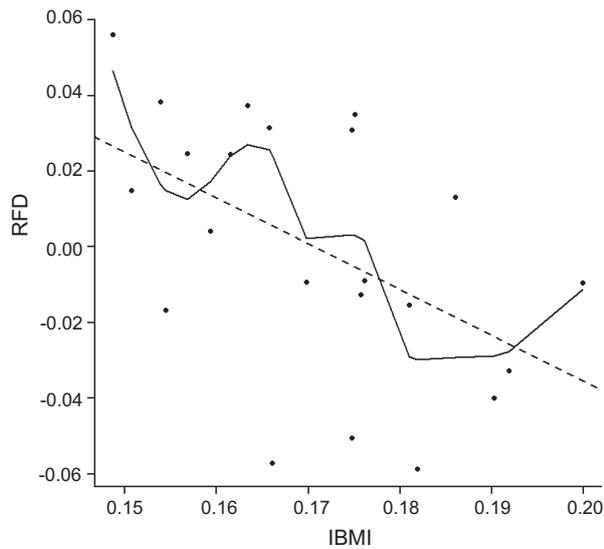


Fig. 2. Relationship between the Relative Fuel Deposition Rate (RFD) and Initial Body Mass Index (IBMI). Dotted line: best fitted linear line; solid line: best fitted line.

(Cicadellidae family) and Diptera (respectively 30.5% and 21.6% of total prey identified). Considering the occurrence, Araneae, Orthoptera (Tettigoniidae, genus *Conocephalus*) and Hymenoptera were well represented (resp. in 31.1%, 29.1% and 15.5% of droppings). Orthoptera and Araneae contributed more to the consumed biomass (64.7% and 13.4%, respectively) than Diptera and Hemiptera (Cicadellidae) (3.8% and 0.3%, respectively). The diet composition of the Aquatic

Warbler did not vary with the age of the individuals (Table 3). The year has a significant effect for two groups: Araneae were significantly more numerous in 2011, and Cicadellidae were significantly more numerous in 2012 (Table 3).

DISCUSSION

Habitat use

Our results on habitat types and areas exploited by the Aquatic Warbler during its post-nuptial migration reinforce the few results available so far on this issue. At the Seine estuary, Provost et al. (2010) showed that areas with low wet vegetation were preferentially selected, while pure reed beds were not. Besides the importance of the presence of water, vegetation heterogeneity appears to be a determinant factor in the habitat selection. This reinforces results of Provost et al. (2010) and Arbeiter & Tegetmeyer (2011) revealing the importance of ecotones largely used by the species and known for hosting a bigger arthropod diversity than dense habitats (Baldi & Kisbenedek 1999). Habitats used during stopover of the post-breeding migration are very close to those exploited during the breeding season (see Tanneberger et al. 2008, 2010, 2013) and on the wintering grounds (see Schäffer et al. 2006, Salewski et al. 2009, Arbeiter & Tegetmeyer 2011), illustrating how the Aquatic Warbler is a habitat specialist highly dependent on particular types of habitat, and how

Table 3. Arthropod groups found in faecal samples of migrant Aquatic Warbler while stopover at the Gironde estuary: number of individuals, occurrence frequency (in %), proportion of total biomass (in %) and factors that influenced the relative prey abundance.

Order	Family/genus	No of individuals (proportion of prey number)	Occurrence (in %)	Biomass (in %)	Year effect	Age effect
Hemiptera	Cicadellidae	65 (30.52%)	56.31	0.31	$F_{1,104} = 9.09$, $p = 0.003$ (2012)	$F_{1,104} = 0.36$, $p = 0.55$
Diptera		46 (21.60%)	42.72	3.77	$F_{1,104} = 0.44$, $p = 0.51$	$F_{1,104} = 1.31$, $p = 0.26$
Araneae		33 (15.49%)	31.07	13.37	$F_{1,104} = 12.61$, $p = 0.001$ (2011)	$F_{1,104} = 1.46$, $p = 0.23$
Orthoptera	Tettigoniidae / Conocephalus	36 (16.90%)	29.13	64.75	$F_{1,104} = 1.18$, $p = 0.28$	$F_{1,104} = 0.53$, $p = 0.47$
Hymenoptera		16 (7.51%)	15.53	8.93	$F_{1,104} = 1.31$, $p = 0.25$	$F_{1,104} = 0.15$, $p = 0.70$
Coleoptera		6 (2.82%)	5.83	3.12	-	-
Heteroptera		4 (1.88%)	3.88	1.36	-	-
Lepidoptera		3 (1.41%)	2.91	2.22	-	-
Homoptera	Aphididae	2 (0.94%)	1.94	0.08	-	-
Gasteropoda		1 (0.47%)	0.97	-	-	-
Zygopytera		1 (0.47%)	0.97	2.10	-	-

it is tracking similar habitats throughout its annual life cycle.

Home ranges of individuals stopping at the Gironde estuary (average \pm s.d. = 6.64 ± 2.64 ha) are not dissimilar to those estimated at another stopover site in France (9 ha in average for the Seine estuary, Provost et al. 2010), on breeding sites (8 ha in average for males and 4 ha for females, Schaefer et al. 2000), and on wintering areas (3.9 ha in average at Djoudj National Park in the center of the Senegal River delta, Arbeiter & Tegetmeyer 2011). The relatively high fragmentation rate of home ranges in the Gironde estuary (C_{part}) is likely to be linked with the high level of habitat selection made by tracked individuals, and the relative discontinuity of habitats suitable for the species.

Stopover duration

The stopover duration, including the estimated time spent by individuals before being first captured, was estimated at approximately 6–7 days, similar to an estimate obtained at another important stopover site in France (6 days at Loire estuary, Chenaud et al. 2011). These values are relatively close to estimates obtained for other reed bed passerines during post-breeding migration: 6.1 days (95% CI 3.0–9.2) for Reed Warbler *A. scirpaceus* in southern France (Montpellier Region; Balança & Schaub 2005), 9.1 ± 5.2 days for Sedge Warbler *A. schoenobaenus* (measured for 17 European and African sites; Schaub & Jenni 2001), and probably nearly 9–10 days for first-year Bluethroats *Luscinia svecica* in Spain (Arizaga et al. 2013). Many environmental factors such as fuel load, refueling rate, stopover opportunities along the migratory route, or meteorological conditions may influence the stopover duration at a particular site (e.g. Bairlein 1985, Biebach et al. 1986, Winker et al. 1992, Morris 1996). Thus it is difficult to make a link between the stopover duration and the quality of stopover sites. As demonstrated by Dunn (2000), the rate at which migratory birds replenish energy reserves during stopover is probably the better indicator of the quality of habitats used.

Fuel deposition

Our results highlight the fact that the Relative Fuel Deposition (RFD) was significantly and negatively influenced by the Initial Body Mass Index (IBMI). The effect of body condition on RFD could be explained by the mechanisms linking foraging behaviours and the baseline corticosterone

levels (BCL). Indeed, even if we did not measure the BCL, we can imagine that lean birds with depleted fat reserves have a higher BCL involving a hyperphagia, whereas adrenocortical responses reduce this behavior when birds increase their body reserves (Long & Holberton 2004). Reducing the foraging behavior while being already stout can be an adaptive strategy to avoid high energy costs due to a high IBMI. The separation method we used to determine “lean” and “stout” groups in our study is arbitrary, nevertheless our result reveals a large difference in the foraging strategy of birds according to their body condition (birds with a low IBMI accumulate 23.43 times more fuel than birds with a high IBMI). This highlights the importance of taking into account the heterogeneity in migrating populations to fully consider the ecological functionality of stopover sites and their importance. Thus, to study the fuel deposition along bird migration routes, it is important to consider that populations on stopover sites may be composed of: (1) individuals with depleted fuel reserves arrived recently on stopover sites after a migration flight or having suffered from bad weather conditions since their arrival, and (2) individuals with better body conditions, stopping only to rest or to wait for better meteorological conditions, or having already locally stored fuel reserves before being captured. We consider that we capture only birds that stopped naturally on the site as playback is not used at night so does not induce stopover.

Diet study

The diet of the Aquatic Warbler highlighted in the Gironde estuary has some similarities with the diet observed in breeding areas (Schulze-Hagen et al. 1989) and on other French stopover sites (Audierne Bay — Kerbiriou et al. 2011; Seine estuary — Provost et al. 2010). For example, in terms of proportion of prey number, Diptera represent 21.6% of the diet composition in the Gironde estuary, 22% in the breeding areas, 38% in Audierne Bay and 27% in Seine estuary. Arachnida are also well represented: 15.5% of the diet composition in the Gironde estuary, 30% in the breeding areas, 14% in Audierne Bay and 6% in the Seine estuary. However, compared to other stopover sites, we highlight the importance of Cicadellidae (30.5%) and the very small amount of Aphidae (0.9% in Gironde estuary, 19% in Audierne Bay and 37% in Seine estuary). Nevertheless, it is difficult to make a conclusion about Aphids because their populations are known to experience high interannual

variability (Day et al. 2010). Like other studies, we noted the importance of large prey such as Orthoptera and Araneae that significantly contribute to the biomass consumed, respectively 64.7% and 13.4%. However in the Gironde estuary the importance of Orthoptera is truly spectacular (see Kerbiriou et al. 2011, Provost et al. 2010).

CONSERVATION IMPLICATIONS

Most of the habitats selected by the Aquatic Warbler have an uncertain future, especially due to coastline dynamics: erosion, siltation, and vegetation changes, but also due to physical constraints in the intertidal zone where, for instance, agricultural polder dikes can avoid a natural shoreline evolution. Thus it is essential to develop management policies which take into account these parameters. For the coming years, on the right bank of the Gironde estuary, creation of shallow water bodies is planned on the sub-halophytic grasslands. The aim of this work is to recreate suitable habitats for the Aquatic Warbler. These approaches could be developed in other areas to optimize the development and the sustainability of favorable habitats for the Aquatic Warbler but also for other species (animal or plants) which can benefit from low wet vegetation, flooded or partially flooded. The French Atlantic coastline is known to host a huge part of the world's population of the Aquatic Warbler during fall migration (Jiguet et al. 2011, Le Nevé et al. 2013). At the same time, 24% of the French metropolitan coastline is receding under the effects of marine erosion. Moreover, natural environments, water bodies, and wetlands constitute more than half of the lands located less than 250 m from receding coastlines (IFEN 2007). Given the erosion risk and rise in water level forecast before the end of the century (between 26 and 82 cm due to the global warming of the planet, IPCC 2013), these considerations reveal that countries such as France need to imagine the future of their coastal wetlands. In the Gironde estuary, the right bank is composed of an important surface of agricultural polders. The erosion we notice along this area starts to compress wetlands used by reed bed passerines against dykes. Given the rise in water level forecast, measures like the giving back of some polders and the creation of water bodies behind dykes could be a solution for long term preservation of wetland surfaces. The surroundings of those new open spaces could be maintained by extensive grazing

which could provide vegetal structures favoring the dynamic of arthropod species like Araneae and Orthoptera (Schmidt et al. 2005), which constitute a large part of the diet of the Aquatic Warbler. Such considerations could be extended to a huge part of the French Atlantic coastline for the conservation of hosting capacity for migratory reed bed passerines like the Aquatic Warbler.

The importance of Araneae and Orthoptera (Tettigoniidae) noticed in the diet of Aquatic Warbler in the Gironde estuary and the relative importance of mosquitoes in the diet of European arachnids (Medlock & Snow 2008) and, to some extent, in the diet of Tettigoniidae (Gangwere 1967), question the potential effects of B.t.i. — *Bacillus thuringiensis israelensis* — used quite significantly on Gironde estuary wetlands and along a very significant part of the French Atlantic coastline to control mosquitoes' populations for human convenience. Indeed, even though this toxin appears to have a targeted action on Culicidae and Chironomidae (Charbonneau et al. 1994), it can affect food webs (Boisvert & Boisvert 2000) and food resources exploited by sensitive species. Negative effects of mosquito control have already been demonstrated on insectivorous breeding bird populations (Poulin et al. 2010). In the Gironde estuary, by reducing the numbers of mosquitoes, this control can diminish the availability of large predators that Aquatic Warblers feed on. Studies on stopover sites could be useful within the context of conservation of French Atlantic wetlands through which the main part of the world's population of Aquatic Warbler migrates during fall migration.

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STRESZCZENIE

[Ekologia wodniczki na miejscu przystankowym w estuarium Żyronda podczas jesiennej wędrówki]

Wodniczka jest jedynym zagrożonym gatunkiem z grupy śpiewających ptaków wróblowych. Podczas wędrówki jesiennej gatunek ten leci wzdłuż atlantyckiego wybrzeża Francji, a estuarium Żyronda (powstałe z połączenia rzek Garonny i Gordogne) jest jego ważnym miejscem przystankowym. W latach 2010–2012 badano w tym miejscu: wielkość areалу, wybiórczość siedliskową, czas pozostawania na miejscu przystankowym, tempo uzupełniania zapasów oraz dietę wodniczki. Ptaki chwyte były w sieci na prawym brzegu Żyrondy przez cały sierpień. W latach 2010–2011 20 osobników wyposażono w nadajniki telemetryczne. Średni czas namierzania ptaków z nadajnikami wynosił 3,35 dnia. Łącznie zebrano dane o 926 lokalizacjach na obszarze o powierzchni 121,21 ha (Fig. 1).

Wykazano, że wodniczki wykorzystywały do żerowania niewielkie arealy. Średnio miały one powierzchnię 6,6 ha, z jednohektarowym terenem głównego żerowiska. Arealy były dość mocno

pofragmentowane. Część ptaków przenosiła się z miejsc schwytania na dalsze tereny estuarium, najdalej 1 940 m od miejsca wypuszczenia (Fig. 1). Ptaki najczęściej stwierdzone były na terenach zalanych lub w strefie pływów porośniętych zróżnicowaną i raczej niską roślinnością, taką jak sitowie lub sitowie z trzcinowiskiem.

Na podstawie wielokrotnych schwytań tych samych osobników wyliczono parametry przeżywalności i prawdopodobieństwa schwytania (Tab. 1–2). Średnia długość okresu pozostawania przez ptaki na miejscu przystankowym wynosiła 6,46 dnia. Analizowano także tempo uzupełniania zapasów tłuszczowych (RDF — relative fuel deposition) oraz wpływ na ten parametr minimalnej długości przebywania na miejscu przystankowym (MLS — minimum length stopover) oraz indeksu masy ciała w czasie pierwszego schwytania (IBMI — initial body mass index). Stwierdzono, że ptaki przylatujące z niewielkimi zapasami uzupełniały je w znacznie szybszym tempie niż te posiadające ich więcej (Fig. 2). W diecie wodniczek na badanym miejscu przystankowym największą rolę odgrywały prosto-skrzydłe, pajęczaki i błonkoskrzydłe (Tab. 3).