FORAGING REQUIREMENT AND DIET SPECIFICITY OF THE GLOBALLY THREATENED AQUATIC WARBLER *ACROCEPHALUS PALUDICOLA* AT AUTUMN MIGRATION STOPOVER SITES.

Christian KERBIRIOU[1], Bruno BARGAIN[2] Isabelle LE VIOL[1], Sandrine PAVOINE[1]

[1] Muséum national d'histoire naturelle - UMR 5173 MNHN-CNRS-UPMC Conservation des Espèces, Restauration et Suivi des Populations, 55 rue Buffon, 75005 Paris France

[2] Bretagne-Vivante Trunvel 29720 Tréogat, France.

Corresponding author:

Christian Kerbiriou

UMR 5173 CERSP

Muséum national d'histoire naturelle

55 rue Buffon

75005 Paris France

Fax: 01 40 79 38 35

E-mail: kerbiriou@mnhn.fr

Keywords : diet, *Acrocephalus paludicola*, *Acrocephalus scirpaceus*, *Acrocephalus schoenobaenus*

Words :

SUMMARY

An effective conservation of the Aquatic Warbler (*Acrocephalus paludicola*), one of the most threatened Western Palaearctic migratory passerines, requires a good knowledge of its ecological needs on stopover sites. In particular, it is crucial to identify the diet of the Aquatic Warbler (preferred arthropod preys), which controls accumulation of fat reserves before migration, to selected and manage adequate protected areas. Another key information need is the relationship between Aquatic warbler's prey abundance and habitats. We performed standardized mist netting during 12 years in Audierne marshes (Western France), which resulted in the capture of 1200 Aquatic Warblers, and permitted measurements of mass gain and collection of faeces to infer birds' diet. Invertebrate sampling was carry out on the three main Audierne marshes (reedbeld, fen mires and meadow). In order to go beyond prey digestibility bias we also study to two close *Acrocephalus* species, present on migration stopover during the same period. The diet composition of the Aquatic Warbler observed on migration stopover sites is that of a specialist species, with large prey sizes (Odonata, Orthoptera, Lepidoptera), specific preys (Odonata, Araneida) and a relatively low diversity of preys. Similarly to Sedge Warblers, Aquatic Warblers put on weight during migration stopover (daily mass gain = 0.34g) suggesting a strategy based on few stopover along the long-distance migration. Due to large differences in diet, conservation management action on stopover sites for the threatened Aquatic Warbler should not rely on existing knowledge for the Sedge and Reed Warblers. Similarities in the diet of the Aquatic Warbler between nesting areas and migration stopover areas and relationship between habitat and prey's abundance, suggest that fen mires play and important role for the quality of stopover foraging habitat.

INTRODUCTION

Decline of long-distance migratory songbirds have been highlight, and the origin appear numerous: climate change and its consequence on phenological response **(**Both *et al.*, 2006**),** degradation of wintering habitat **(**Robbins *et al.*, 1989**)** and many studies has also shown that high-quality stopover habitats and a preserved network of stopover are critical links between breeding and wintering areas for many species, and their preservation should be considered an essential component of strategies aiming to conserve migratory bird populations (Russell *et al.*, 1994, Moore *et al.*, 1995, Ktitorov *et al.*, 2008).

The Aquatic Warbler (*Acrocephalus paludicola*), is a rare long-distance migratory birds and is considered as one of the most threatened Western Palaearctic migratory passerines (Collar *et al.* 1994). This species population had suffered an important decline mainly because of breeding habitat loss (Dyrcz & Zdunek 1993, Kozulin *et al.,* 2004). Furthermore along its migratory way important loss of marshes areas (stopover migration habitat) have occurred: 40% of reedbed habitats were lost between the years of 1945 and 1990 in United Kingdom (Biodiversity Action Plan 2008) ; 50% of marshes areas in France were loss between 1970 and 1990 (Bernard 1994) ; In Netherlands the National Wetlands Inventory evaluated that 40% of freshwater wetlands had been destroyed or degraded by human activities in only a 10-year period (Holland *et al.*,1995).

As many species of insectivorous birds that breed in northern Europe and winter in sub-Saharan Africa, the Aquatic Warbler has to cross wide ecological barriers (e.g. seas or deserts), which requires long uninterrupted flights fuelled by large fat deposits. Migration strategy, including departure date, flight duration and range, or habitat and diet selection, is known to be under considerable selection pressure (Bibby & Green 1981, Bairlein & Totzke 1992). In particular, all migratory species depend crucially on the existence of suitable feeding areas to accumulate fat reserves before and during migration (Berthold 1975). Northern Aquatic Warbler populations migrate through Western Europe in autumn, visiting marshes in the Netherlands, Belgium, France and to a lesser extent the United Kingdom (de By 1990, Julliard *et al.,* 2006). France appears to host the largest number of individuals (Julliard *et al.,* 2006), exclusively in the western coastal regions (mostly Normandy, Loire Valley and Brittany). This country should therefore play a central role in the conservation of the Aquatic Warbler, for example by protecting adequate habitats to provide stopover sites on the species migration routes (Julliard *et al.,* 2006).

As highlighted in the European Action Plan (Heredia 1996), an efficient conservation of such threatened migratory passerine requires a thorough description of its ecological needs in stopover sites. As far as we know, few studies have dealt with Aquatic Warbler's diet, and moreover have focused on the breeding period only. And unfortunately, the ecological needs and the network of stopover sites of the Aquatic Warbler cannot be derived from information on congeners, as species within a genus can exhibit very different migration strategies (Bibby & Green 1981).

We believe that identifying preys of the Aquatic Warbler, which are crucial for accumulation of fat reserves, is key to target appropriate habitats for conservation. Direct observation of Aquatic Warbler feeding on stopover is hardly seems possible due to rarity of such observation (rarity of this bird, observation distance and visibility in such marshes habitat) and indirect study of diet through faeces analysis is hindered by differential preys digestibility. However comparing in the same stopover area faeces of the Aquatic Warbler and two commoner congeners (Reed Warbler: *Acrocephalus scirpaceus* and Sedge Warbler: *Acrocephalus schoenobaenus*) could allow highlight diet specifity of the Aquatic Warbler according to the hypothesis that digestibility bias is equal among these three close species. We then identified the taxa that make a major contribution to the diet of each species and secondly the taxa that distinguish the diet of the Aquatic Warbler from two other warblers. To go further, we studied the relationship between Aquatic Warbler main preys and habitat.

With classical recovery data provided by ringing scheme (bird ring in a site and recapture or found dead in other site), we could not expected in mid term gather sufficient data for described the Aquatic Warbler migration strategy. Moreover this could not be directly derived from strategy known on congeners. However a comparative approach of mass gain strategy in the same stopover area for the Aquatic Warbler and two commoner congeners known to exhibit differential strategy could be fruitful. The strategies to cover long migratory distances differ among species. Some like the Reed Warbler are known to move in many short steps, others, like the Sedge Warbler negotiate the same distance in few jumps with very long flights (Bibby & Green 1981). Consequently, the physiological requirements, and the ecological and time constraints are rather different. Moving by a series of short flights requires smaller fat reserves on board. Mass gain strategy of the Aquatic Warbler in regards of the Reed and Sedge Warbler is then expected inform us on its strategies to cover long migratory distances. This information is of conservation concern because moving by a series of short flights requires smaller fat reserves on board it requires many different suitable stopover sites en route. In this case the disappearance of one site is less dramatic, as these 'hoppers' can easily move to the next site. Whereas for species exhibiting long hauls flights strategy, the disappearance or degradation of one important particular stopover site would seriously impair the migration.

METHODS

Focal species

The Aquatic Warbler (*Acrocephalus paludicola*), is a globally threatened species (Collar *et al.*, 1994) whose breeding range has shrunk dramatically during the last decades: the species has disappeared from its former breeding grounds in France, Belgium, the Netherlands and Austria (Bargain 1999). The European population contains between 13,000 and 21,000 singing males, most of which are found in Belarus, Ukraine and Poland (Aquatic Conservation Team 1999). Despite yearly fluctuations, there is strong evidence that the Aquatic Warbler population keeps declining in Europe (Aquatic Warbler Team 1999, Kovacs & Vegvari 1999, Kozulin & Flade 1999, Birdlife International 2004),

Study area

The study was carried out in Audierne Bay marsh (Western France W4°19'14,0229 N47°55'15,0881). In Audierne marsh the three main vegetation succession, from littoral lake are reedbed (dominated by stand of the common reed *Phragmites australis*, wherein the water table is above the ground level for most of the year), fen mire are medium herbaceous vegetation (up to 1 meter), with in summer the water table only few centimetres above to the ground level or sometime dry up. This vegetation is dominated by a great number of plant species (*Scirpus spp*, *Juncus ssp*, *Eleocharis spp*, *Iris pseudacorus*, *Oenanthe spp*) and the third habitat is hygrophilous meadow grazed extensively, dominated by *Agrostis spp*, *Dactyle glomerata*, *Rumex spp*,.

Between 1988 and 2006, we performed standardized mist netting, which result in the capture of up to 60,000 Sedge Warblers, 26,000 Reed Warblers, and 1200 Aquatic Warblers. This area is known as an important stopover site for Sedge Warblers, hosting above 2% of the breeding population (Bargain *et al.*, 2002), but is also an important regional breeding ground for the Reed Warbler (Bargain & Henry 2005). Recapture of banded Sedge Warblers in Audierne marsh indicate that these birds breed in Ireland, the United Kingdom, the Netherlands, Belgium, and Norway.

Faecal analysis

Birds' diet was assessed by faecal analysis. Between 2001 and 2004, we collected 128 78 and 28 independent samples of Aquatic, Sedge and Reed Warbler faeces, respectively, during ringing operations in August and September; most samples were collected in August 2003 (Table 1). To collect faeces, we placed birds in special bags with a plastic-coated bottom, fifteen min. before their release. Faeces samples were stored in alcohol and dissected under a binocular microscope (magnification 15x to 45x). Identifiable chitinous fragments were counted in each sample, and pooled to estimate the minimum number of individuals of each taxonomic group (e.g. four Odonata wings were counted as one individual). This method likely biases diet evaluation, since soft-bodied or small preys are less readily detected. However, Davies (1977) showed that there is a strong correlation between prey remains in the faeces and the composition of the true diet in other insectivorous passerines, so that the method used here is expected to provide an accurate picture of diet.

Identifying the specificity of the Aquatic Warbler diet

We first conducted a Canonical Correspondence Analysis (CCA), which is a constrained ordination method developed to relate community composition to known variation in the environment, to evaluate the contribution of each prey species to diet composition of the Aquatic, Reed and Sedge Warblers (ter Braak 1986, Palmer 1993). Furthermore we used the apportionment of quadratic entropy (APQE), an analysis which allows diversity decomposition according to a given hierarchy, (Pavoine & Dolédec 2005). Here the hierarchy comes from *Acrocephalus* faeces and prey species in each faeces. This analysis allows variation testing within samples (faeces) and within Acrocephalus species. The significance of these diversity components is test by comparing the observed distributions with those expected to arise by chance using a simulation approach with 999 permutations. Programs and functions for computing quadratic entropy on R sofware environment are available on request to Sandrine Pavoine. According that diet data mostly come from one month in one year (Table 1) we restricted these analysis (CCA and APQE) on August 2003 diet data, nevertheless similar results were obtained with the full data set.

Relationship between Aquatic Warbler's preys and habitat

With the aim to improve our knowledge of the Aquatic Warbler foraging habitat selection, we first attempt to assess the level where Aquatic Warbler forages in the vegetation. We then , jointly used three semi-quantitative invertebrate sampling methods and focussed on spiders group. We choose pitfall trap, with non attractive conservative liquid, in order to assess invertebrate density-activity in the ground (2 stations per habitat, 3 pitfalls per station, from the 3 July 2002 to the 13 September 2002), yellow blow trap for invertebrates present in medium level of vegetation (2 stations per habitat, 1 blow trap per station, collect after 4 days of functioning, for a total of 15 sampling per habitat) and standardized sweep net in order to collect invertebrate in the high part of the vegetation (2 sampling per habitat, walking on a 25 meters distance, do the same day (1/08/2002) for the 3 habitats). Through this sampling we focussed our study on spiders preys species due to the relationship between spiders families, functional group and vegetation level.

In a second step we evaluate the availability of the main prey's Aquatic Warbler's preys among the three main habitats present in Audierne marsh (reedbed, fen mire and hygrophilous pasture grazed extensively) using the same invertebrate sampling design. Variations of the different prey's abundance were calculated using linear regressions model (GLM).

Comparing the diet diversity of Aquatic, Sedge and Reed Warblers

We studied the variation in prey diversity within each species' diet. We first used Simpson's Diversity Index (D) (Hill 1973), which measures the probability that two preys randomly selected from a sample belong to the same taxonomic group. Hence, larger D values reflect smaller diversities. This index accounts for both number and abundances of species, so that rare species contribute little to the total diversity.

By using Simpson's diversity index on raw data to compare diets, we assume equal detectability of all prey species, a hypothesis which is probably not met (Boulinier *et al.*, 1998; Nichols *et al.*, 1998). To correct for heterogeneous species detection probabilities, we therefore used statistical methods derived from capture-recapture approaches developed in population: individual are changed by species and then instead of assess population size this approach provide an estimator of community size, here prey species richness. Prey species richness was estimated with the jackknife estimator of Burnham and Overton (1979). As in many recent studies (Doherty *et al.*, 2003; Selmi & Boulinier, 2003; Lekve *et al.*, 2002; Stenseth *et al.*, 2002; Kerbiriou *et al.*, 2007) addressing richness estimation from species count data, we used program COMDYN (Hines *et al.*, 1999). This program allows assess estimate richness and probabilities of detection of species. As Reed Warblers had far smaller sample sizes than the two other species, we performed 50 random re-sampling within faeces samples of each species to obtain identical sample sizes (n = 10 faeces). For each species, each of 50 random re-samplings was input into program COMDYN to obtain estimates of prey species detectability and richness.

Comparing mass gain strategies during stopover

To compare mass gain strategies across the three Warbler species, we analyzed changes in body mass between capture/recapture events within a same year and stopover site. Between 1988 and 2006, ringing operations were conducted during the post breeding migration period: from early July to late September at the ornithological station of Audierne marsh, using standardized mist netting in the reed bed (see Bargain *et al.*, 2002 and Bargain & Henry 2005). Whenever weather was enough fine the ringing station was open, for a total of 77 days efficient per year (SE ± 4 days; extreme: 44 ; 115). Each captured bird was ringed, weighed and aged (two classes: adult and juvenile, i.e. born within year). When birds were captured several times within a day, we retained the first measure only. For birds captured more than once, we recorded the change in body mass between two capture events (the vast majority of individuals were recaptured only once, which generated one data point per individual). At Audierrne marshes, we collected a total of 3517 such body mass changes for the Sedge Warbler, 2611 for the Reed Warbler and 50 for the Aquatic Warbler. We used Generalized Linear Models to explore the relation between body mass change and the number of days between two capture events, as well as the effect of bird age and year on mass gain. As possible difference of mass gain are expected exist between juvenile and adult, we used relative mass gain (*G'*) instead off gross mass gain (i.e. the within year difference between the mass measured during the recapture and the mass measured during the previous capture).

$$G' = \frac{(Mr - Mc)}{Mc}$$

Where *Mc* is the mass measured during the first capture and *Mr* is the mass measured during the recapture.

According that Audierne marshes are an important regional breeding ground for the Reed Warbler we test the relation between body mass change and the number of days on the whole dataset of Reed Warbler and in a second step only on the birds (n=23) which the foreign origin was known (birds ringed during the breeding season in an other country). For the Aquatic warbler we also used the whole national data in order to test the existence of regional difference of mass gain. Complementary data come from Sandouville (W0°19'15,0462 N49°29'51,3665), Chenac-Saint-Seurin-d'Uzet (W0°49'58,8482 N45°29'59,6687) and Frossay/Le Massereau (W1°55'54,9121 N47°14'41,8772) due to the similarity of the standardized mist netting protocol.

RESULTS

Taxa that make a major contribution to the diet of Aquatic, Reed and Sedge Warblers.

In the faeces samples, we recorded a total of 1731 preys, few of which could be identified to species level. In terms of prey abundance, the diet of the Sedge Warbler appeared to be dominated by Aphids (67%), followed by Diptera (17%), whereas the Aquatic Warbler's and Reed Warbler's diets were dominated by Diptera (38 and 54%, respectively) and Aphids (21 and 22%, Table 2). Using a predictive model of the relationship between body length of invertebrate groups and their mass (Ganihar 1997), the contribution of Odonata, Araneida, Orthoptera, Diptera and Lepidoptera to consumed biomass was respectively 43%, 13%, 12% 9% and 8% for the Aquatic Warbler, for the Reed Warblers Diptera represent 33%, Aphids 16% and Hymenoptera 15% and for the Sedge warbler Aphids represent 48%, Odonata 12%, and Diptera 10% (Table 2).

Specificity of the Aquatic Warbler's diet

With the aim to identify the taxa that distinguish the diet of the Aquatic Warbler from Reed and Sedge Warblers, we performed a Canonical Correspondance Analysis (CCA). Lepidoptera, Araneida, Orthoptera, Odonata, Coleptera Atlidae contributed to discriminate the Aquatic Warbler diet from that of the two other Warblers (Fig. 1). Aphids contributed mainly to the Sedge Warbler's diet while wasps and, to a lesser extent, flies contributed to the diet of the Reed Warbler (Fig. 1). This difference in diet compositions among Warbler species was significant, as suggested by the APQE analysis (P = 0.001), whereas no significant variation in composition was detected among faeces samples within species (P = 0.920)

Availability of the Aquatic Warbler's preys among habitats.

Spiders families distribution among the different sampling methods used (Fig. 2), show that the most abundant spiders families found in the Aquatic Warbler's diet (*Clubionidae, Tetragnathidae*, *Araneidae*) were collected mostly with sampling methods designed for inventory high level of vegetation (sweep net). Furthermore, the availability of the fourth principal prey's in term of biomass (Odonata, Orthoptera and Araneida: *Clubionidae, Tetragnathidae, Araneidae*) varied across habitat (Fig. 3). Abundance of Araneida are significantly lower in pasture and reedbeld than fen mire whatever the sampling methods used ($P < 0.0001$), the same pattern is observed for the abundance of Odonata ($P < 0.01$ for blow trap and $P < 0.0001$ for sweep net). Abundance of Orthoptera are high in both fen mires and pastures, this latest habitat present significant higher abundance when blow trap sampling was used (P = 0,005) but no difference could be detected when sweep net sampling was used (P = 0,71). Abundance of Diptera in pasture and fen mire was higher (P < 0.001) than reedbeld, and the abundance in pasture slightly higher than fen mire (P =0.03). Lepidoptera (moth) were almost exclusively collected in fen mires.

Diet diversity of the Aquatic, Sedge and Reed Warblers

Significantly fewer preys were found in Aquatic Warbler faeces (4.9 preys per faeces sample; se = 0.4) than in Reed Warbler (6.2 preys; se = 0.8) and Sedge Warbler (13.2 preys; se = 1.7) faeces ($F_{2,218}$ = 19.33 , P < 0.0001). Similarly, prey species richness was generally lower in Aquatic Warbler faeces (2.84 species per faeces sample; se = 0.15) than in Reed Warbler (3.07 species; se = 0.33) and Sedge Warbler (3.10 species; se = 0.16) faeces. Finally, prey species diversity was also lower in Aquatic Warbler faeces than in Reed Warbler and Sedge Warbler faeces (Simpson's Diversity Index D = 0.84, 0.70 and 0.53 respectively).

To further compare the three Warblers' diets and account for heterogeneous sample sizes, as well as potential variation in prey detectability, we estimated species richness in faeces samples using resampling (to correct for sample size, see "Methods") and COMDYM software. As before, the Aquatic Warbler had a less diversified diet (16.89 species (se = 1.34) on average in 10 faeces), than the other two Warbler species (Reed Warbler: 22.24 species; se = 2.45; Sedge Warbler : 28.75 species ; se = 4.63 ; $F_{2,147}$ = 4.92, P = 0.009). Interestingly, this difference is likely not due to among-Warbler species differences in prey detection probabilities: the average detection probability was generally high (0.77; se = 0.07 for the Aquatic Warbler, 0.72; se = 0.02 for the Reed Warbler and 0.72; se = 0.04 for the Sedge Warbler) and not significantly different across Warbler species ($F_{2,147}$ = 1.58, P = 0.20).

Finally, Aquatic Warblers consumed larger preys (average 9.2mm; se = 0.5) than Reed (5.1mm; se = 0.3) and Sedge Warblers (4.6mm; se = 0.3) (Fig. 2; $F_{2,216}$ = 30.14, P <0.0001).

Differences in mass gain strategies of the Aquatic, Sedge and Reed Warblers during stopover.

Significant difference in mass between age class have been detected for the Sedge Warbler (10.97g ± 0.02 for juvenile and 11.98g ± 0.09 for adult $F_{1,3514}$= 197.78 ; P < 0.0001); and the Reed Warbler (10.92g ± 0.02 for juvenile and 11.19g ± 0.05 for ≥ 1 adult $F_{1,2724}$= 19.55 ; P < 0.0001) but not for the Aquatic Warbler ($F_{1,79}$ = 1.33 ; P = 0.25), probably due to the small sample size for the latest species. Then, except for the estimation of the daily mass gain mean, all the analysis have been carried out on relative mass gain (G’). According to statistical result (trend and probabilities) analysis carried out on relative mass gain (G’) converge with preliminary analysis carried on gross mass gain.

No interaction between the number of days between two capture events and birds age class have been detected for any of the three Warbler studied (Aquatic Warbler $F_{1,46}$ = 2.02 ; P = 0.16; Sedge Wabler $F_{1, 3501}$ = 0.279 ; P = 0.59 ; Reed Warbler $F_{1,2709}$ = 0.44 ; $P=0.51$).

No correlation between the relative mass gain (G’) and number of days spent was detected for the Reed Warbler (Table 3, Fig. 4). As there is probably a small proportion of local Reed Warbler breeder captured and recaptured that could have induce bias because they were not in migration behaviour, we performed the same analysis but only on a subset of data including only Reed Warbler known to be in migration due foreign ring identities. Again no correlation could be detected ($F_{1,20}$ = 2.38 ; P = 0.11 and moreover the trend was slightly negative -0,05g/days)

In contrast to the Reed Warbler, the relative mass gain (G’) of the Sedge and Aquatic Warblers increased as a direct function of the number of days spent on Audierne marshes migration stopover (Table 3, Fig.4). According to the gross mass gain the mean daily mass gain was 0.22g for the Sedge Warbler and 0.34g for the Aquatic Warbler but this difference was not significant ($F_{1,3563}$ = 0.74 ; P = 0.38).

When all French data of Aquatic Warbler mass gain are considered, no impact of year nor age is detected (respectively $F_{16,62}$ = 1.04 ; P = 0.42 and $F_{1,62}$ = 0.37 ; P = 0.55 ; each variable adjusted to the other variables) neither any variation ($F_{1,77}$ = 1.38 ; P = 0.26) among the main sites where Aquatic Warbler are captured (Audiern Bay marsh, Sandouville, Chenac-Saint-Seurin-d'Uzet and Frossay/Le Massereau). However, the same pattern of mass gain in relation to stopover duration as observed in Audierne is noticed ($F_{1, 62}$ = 29.99 ; P < 0.0001)

In the same way, the test of daily mass gain distribution of Sedge and Aquatic Warblers did not differ significantly (Kolmogorov-Smirnov Goodness-of-Fit Test ks = 0.1543, P = 0.1856)

Mass gain varied significantly across years for the Sedge and Reed Warblers (Table 3). Yet, there was no sign of unconditionally good or bad years, as yearly differences depended on species: daily mass gain was significantly larger in 1993, 2000, 2003 and 2004 for the Sedge Warbler, but significantly lower in 1991, 1994, 2000, 2002, 2003 and 2005 for the Reed Warbler. Daily mass gain was affected by bird age only for the Reed Warbler (Table 3), with a smaller gain for younger individuals.

DISCUSSION

Diet specificity

The diet composition of the Aquatic Warbler observed on the migration stopover site at Audierne Bay marsh is similar to that observed by Shulze-Hagen *et al.,* (1989) in the species breeding areas: the diet consists predominantly of Araneida, Diptera and Coleoptera (30%, 22% and 15% respectively in Shulze-Hagen's study vs. 14%, 38% and 6% in this study). Small numbers of larger prey species such as Orthoptera, Lepidoptera, Odonata are also reported in both studies. Both studies also concur on the average large size of preys: 9.2mm at Audierne marshes vs. 8.4mm (Shulze-Hagen *et al.,* 1989) or 12.1mm (Leisler 1985) in breeding sites. The major difference between the two studies is the presence of caterpillars in Shulze-Hagen's study, whereas none were detected here, which is probably due to a scarcity of such preys in late summer, when Aquatic warblers visit the stopover site. Although large preys are found in small numbers in the Aquatic Warbler’s diet, they are likely to contribute significantly to the total consumed biomass: using we showed that the expected contribution of the contribution of Odonata, Araneida, Orthoptera, Diptera and Lepidoptera to consumed biomass was respectively 43%, 13%, 12% 9% and 8% , whereas as these three first taxa represented only ca. 25% of individual preys, These results should however be interpreted cautiously, notably because of potential differences in prey digestibility.

Similarly, the diet composition of the Sedge Warbler estimated on the stopover site of Audierne Bay marsh closely resembles that observed in other studies. The large contribution of Aphids was already observed in the diet of Sedge Warblers on breeding areas in Southern Finland (Koskimies 1991, Koskimies & Saurola 1985), Estonia (Leivits & Vilbaste 1990), and the Kaliningrad Region (Chernetsov 1998, Chernetsov & Manukyan 2000) and on migration stopover in France (Bibby & Green 1981),. However, note that Koskimies (1991) and Chernetsov & Manukyan (2000) claimed that, despite the observed Aphid-centered diet, the Sedge Warbler is a generalist species rather than an exclusive Aphid specialist. In fact, a lot of alternative preys have been inventoried, such as Diptera, Coleoptera, Hymenoptera, and Araneida, which is consistent with our results: among the three Warbler species, the Sedge Warbler’s diet presented the highest prey species richness estimate. However, observed Aphid outbreaks around the study site (Bargain *et al.,* 2002) are consistent with years of increased mass gain for the Sedge Warbler.

The Reed Warbler also exhibited a diverse diet, which was however centred on Diptera and, to a lesser extent Aphids and Hymenoptera. Such diet composition in the Reed Warbler was also observed by Bibby & Green (1981) in France, Evans (1989) in Wales and the UK, Grim

& Honza (1996) and Grim (2006) in Czech Republic and Rguibi Idrissi et al. (2004) in Moroco. Once again, average prey size in the Reed Warbler's diet measured in this study (5.1mm) was close to that observed by Leisler (1985, 5,4mm) in Poland and Rguibi-Idrissi et al. (2004, 4.5 to 5.4 mm) in Morocco.

Similarity between observed diet in Audierne marshes and literature seem highlight specificity of these Warbler species. Relative to the two congeners species studied Aquatic Warbler appear to be a more specialist specie, as indicated by larger prey size and specialization on Orthoptera, Lepidoptera and Odonata, whereas the Reed and Sedge Warblers have a more generalist diet. In regards to the Aquatic warbler diet, most of its main preys occurred with higher abundance in fen mire and secondary in pasture than reedbeld.
The occurrence of the differents spiders families found in Aquatic Warbler (*Clubionidae, Araneidae,* and *Tetragnatidae*) indicated that Aquatic Warbler foraged in high level of vegetation, according to families' functional group requirements (Roberts 1985) and sampling methods results (Fig.2).

Mass gain

Mass gain strategies are very close for the Aquatic and Sedge Warblers: they both exhibited a significant increase in body mass during their stopover, suggesting accumulation of fat reserves. This conclusion ties in with previous studies of migration patterns, which all suggest that the migration strategy of the Aquatic Warbler is closer to that of the Sedge Warbler than to that of the Reed Warbler (Julliard *et al.,* 2006). Sedge Warblers, which migrate earlier and more rapidly, seem to accumulate fat in Northern France or Southern England and fly almost directly to West Africa over Iberia. In contrast, Reed Warblers migrate more slowly, thus over a longer period and break up the journey by refuelling in Spain and Portugal (Bibby & Green 1981). However, although both Aquatic and Sedge Warblers share refuelling stopovers in Channel and Atlantic littoral marsh complexes, more precisely in Western France for the Aquatic Warbler, Julliard *et al.*, 2006), this study showed significant differences in foraging strategies.

Conservation concerns

In regard to diet specifity of the Aquatic Warbler the choice and management of protected stopover areas for the threatened Aquatic Warbler cannot be based only on existing knowledge regarding the Sedge and Reed warblers' diet. Moreover, according to mass gain strategy and first knowledge on stopover network of the Aquatic Warbler, (important refuelling on few stopover migration) this species is then expected to be more impacted by degradation or loss of some important refuelling stopover migration. It is known that, during the nesting period, the Aquatic Warbler is a true stenotopic species, preferring fen mires that are characterized by mesotrophic to poor eutrophic level, water table near the soil surface and intermediate vegetation height and density (Kozulin & Flade 1999, Kloskowski & Krogulec 1999, Kovacs & Végvari 1999, Schaefer *et al.*, 2000, Kozulin *et al.*, 2004). Due to technical constraint, i.e. mist netting could set up in fen mires or meadow, we were only able to capture Aquatic Warbler on reedbeld then certainly this habitat is important for the stopover, but our study underlined that several preys species occur with higher abundance in fen mires. According that fen mires habitats present at Audierne marshes are close to breeding habitat we could then expected that Aquatic Warbler foraged also in this habitat. Even in the unlikely case where fen mires would not be used directly for foraged by the Aquatic Warbler this habitat play an important role: allowing the complete cycle of life for Aquatic Warbler's prey. Such vegetation is known to maximize the abundance of the large orthoptera prey *Conocephalus discolor* (Baldi & Kisbenedek 1997, Szövényi 2002, this study) and the densities of Clubionidae and Tetragnathidae (Cattin *et al.*, 2003, this study).

The main threats for these habitats, except direct human destruction such as drainage, are the overgrowing of open wetlands by shrubs and reed vegetation (Kloskowski & Krogulec 1999). In French Atlantic stopover sites, consisting mostly of large areas of Common Reed (*Phragmites autralis*), conservation measures should therefore maintain areas of medium vegetation, such as sedge. Restoration management, such as clearing, should focus on marsh edges which are often colonised by schrub willow associated with Common Reed. However, reed cutting, especially extensive cutting for commercial reasons, appears to affect the arthropod communities, with e.g. observed decreases in some passerine bird preys such as Coleoptera and Araneida together with increases in other preys such as Aphids and large spider species (Schmidt *et al.*, 2005). To minimize negative effects, reed cutting should be restricted to small areas, connected with uncut areas, which allows arthropods recolonization (Schmidt *et al.*, 2005). In addition, the creation of small ponds close reedbeds is expected to provide habitat patches with exceptional densities of Diptera (Dolichopodidae and Syrphidae, Brunel *et al.* 1998) and Odonata.

Acknowledgments

Mist-netting operation on Audierne marshes was only made possible thanks to the help of many volunteers of the 'Bretagne Vivante' association, as well as volunteer bird ringers, especially: Olivier Allenou, Gilles Balanca, Jean Claude Barbrault, Olivier barricault, Yves Beauvallet, Jacques Besnault, Marc Bethmont, Thomas Biteau, Bob Burrridge, Marie-Françoise Canevet, Pascal Cavallin, Gérard Chaussi, Olivier Claessens, Jean Louis Clavier, Alejandro Conde, Patrick Damias, Gaëlle Deperrier, Alain Desnos, Philippe Dubois, Patrice Durrafort, Gilles Faggio, Jean-François Fleury, Mathieu Fortin, Cécilia Fridlender, Alain Gentric, Yvon Guermeur, Jacques Hamon, Claude Ingouf, Guy Jarry, Cécile Jolin, Stéphane Jouaire, Alain Leroux, Vincent Lieron, Guy lorcy, George Oiloso, Pascal Provost, Sébastien Provost, Graham Roberts, Peter Rock, Alfred Texier, Alain Thomas, Conrad Thomas, Jean Paul Thomas, Maxime Zucca. Furthermore we would like thanks Patrick Frebourg, Gilles Le Guillou, Frédéric Baroteaux, Yves Beauvallet, Olivier Benoist, Bernard Caillaud, Laurent Demongin, Bruno Dumeige, Patrick Frebourg, Philippe Gautier, Gérard Goujon, Claude Ingouf, Gilles Le Guillou, Joël Pigeon, Jo Pourreau, Jean Pineau, Pascal Provost, ringers working for the Museum and which provided Aquatic Warbler data elsewhere than Audierne marshes. Thank to Olivier Dehorter for the extraction of these data from the Museum ringing database. Finally we thank Romain Julliard, Jean-Pierre Moussus and Emmanuelle Porcher for providing us sound advice on an earlier version of this manuscript.

This study received the financial support of the French Ministry in charge of the Ecology and the Centre National de la Recherche Scientifique, and is part of the life project 'Conservation du phragmite aquatique en Bretagne', no. LIFE04NAT/FR/000086REV.

REFERENCES

Aquatic Warbler Conservation Team (1999). World population, trends and conservation status of the Aquatic Warbler *Acrocephalus paludicola. Vogelwelt* 120: 65-85.

Bairlein, F. & Totzke, U. (1992). New Aspects on Migratory Physiology of Trans-Saharan Passerine Migrants. *Ornis Scandinavica* **23**: 244-250.

Baldi, A. & Kisbenedek, T. (1997). Orthopteran assemblages as indicators of grassland naturalness in Hungary. *Agriculture, Ecosystem and Environment* **66**: 121-129.

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.

Bargain, B. & Henry, J. (2005). Les oiseaux de la baie d'Audierne. Analyse des données de la station de baguage de 1988 à 2003. *Penn ar Bed* 72 p.

Bargain, B., Vansteewegen, C. & Henry, J. (2002). Importance des marais de la baie d'Audierne (Bretagne) pour la migration du phragmite des joncs *Acrocephalus schoenobaenus. Alauda* **70**: 37-55.

Bernard, P. (1994). *Rapport d'évaluation sur les politiques publiques en matière de zones humides* publié [http://www.ramsar.org]

Berthold, P. (1975). Migration: control and metabolic physiology. In Farner, D.S. & King, J.R. (eds) *Avian Biology* Academic Press, New York pp. 77-128.

Bibby, C.J. & Green, R.E. (1981). Autumn migration strategies of Reed and Sedge Warblers. *Ornis Scandinavica* 12: 1-12.

Biodiversity Action Plan. (2008). Reedbeld [http://www.ukbap.org.uk]

Birdlife International. (2004). Birds in Europe. *Population, Estimates, Trends and Conservation Status*. Birdlife Conservation Series 12 Cambridge: Birdlife International.

Both, C., Bouwhuis, S. Lessells, C.M. & Visser, M.E 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**: 81-83

Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.H., Flather, C., Pollock, K.H. (1998). Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Ecology* **95**: 7497-7501.

Brunel E., Cadou D., Kerbiriou C. & Le Viol I. (1998). Les Dolichopodidés et les Syrphidés des îles de la « réserve de Biosphère » d'Iroise (Finistère, France) : premier inventaire (Diptera). *Bulletin de la société entomologique de France* **103**: 57-62.

Burnham, K.P., Overton, W.S. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60: 927-936.

By (de), R.A. (1990). Migration of Aquatic Warbler in Western Europe. *Dutch Birding* **12**: 165-181.

Cattin, M.F., Blandenier, G., Banašek-Richter, C. & Bersier, L.F. (2003). The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities *Biological Conservation* **113**: 179-188

Chernetsov, N. (1998). Diet of Sedge Warblers *Acrocephalus schoenobaenus* during autumn migratory season. In Adams, N.J. & Slotow R.H. (eds) Proc. 22nd Int. Ornithhol. Congres., Durban. *Ostrich* **69**: 369.

Chernetsov, N. & Manukyan, A. (2000). Foraging strategy of the Sedge Warbler (*Acrocephalus schoenobaenus*) on migration. *Die Volgelwarte* **40**: 189-197.

Collar, N.J. Crosby, M.J. & Stattersfield, A.J. (1994). *Birds to Watch 2. The World List of Threatened Birds*. Birdlife Conservation Series 12. Cambridge: Birdlife International.

Davies, N.B. (1977a). Prey selection and the search strategy of the Spotted Flycatcher *Muscicapa striata*, a field study on optimal foraging. *Animal Behaviour* **25**: 1016-1033.

Davies, N.B. (1977b.) Prey selection and social behaviour in wagtails (Aves: Motacillidae). *Journal of Animal Ecology* **46**: 37-57.

Doherty, P.H., Sorci, G., Royle A., Hines, J.E., Nichols, J.D., Boulinier, T. (2003). Sexual selection affects local extinction and turnover in bird communities. *PNAS* **100**: 5858-5862.

Dyrcz, A. & Zdunek, W. (1993). Breeding statistics of the Aquatic Warbler *Acrocephalus paludicola* on the Biebrza marshes, northeast Poland. *Journal für Ornithologie* **134**: 317-323.

Evans, M.R. (1989). Population changes, body mass dynamics and feeding ecology of Reed Warbler *Acrocephalus scirpaceus* at Llangorse Lake, South Powy. *Ringing & Migration* **10**: 99-107.

Ganihar, S.R. (1997). Biomass estimates of terrestrial arthropods based on body lenght. *J. Biosc.* **22**: 219-224.

Grim, T. & Honza, M. (1996). Effect of habitat on the diet of Reed Warbler (*Acrcephalus scirpaceus*) nestling. *Folia Zoologica* **45**: 31-34.

Grim, T. (2006). An exceptionally high diversity of hoverflies (Syrphidae) in food of the Reed Warbler (*Acrcephalus scirpaceus*). *Biologia* **61**: 235-239.

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 Plan: 327-338. Strasbourg: Council of Europe.

Hines, J.E., Boulinier, T., Nichols, J.D., Sauer, J.R.s Pollock, K.H. (2003). COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study* **46**: 209-217.

Holland, C.C., Honea, J., Gwin, S.E., Kentula, M.E. (1995). Wetland degradation and loss in the rapidly urbanizing area of Portland, Oregon *Wetlands*. **15**: 336-345.

Julliard, R. Bargain, B, Dubos, A. & Jiguet, F. (2006). Identifying autumn migration routes for the globally threatened Aquatic Warbler *Acrocephalus paludicola*. *Ibis* **148**: 735-743.

Kerbiriou, C., Le Viol I., Jiguet, F.& Julliard, R. (2007). The impact of human frequentation on coastal vegetation in a Biosphere Reserve. *Journal of Environmental Management in press*

Koskimies, P. (1991). *Acrocephalus schoenobaenus* (Linaeus 1758) Schilfrohränger. In Glutz von Blotzheim, U.N. & Bauer, K.M. (eds) *Handbuch der Vögel Mitteleuropas.* Aula-Verlag, Wiesbaden, pp: 291-340.

Koskimies, P. & Saurola, P. (1985). Autumn migration strategies of the Sedge Warbler (*Acrocephalus schoenobaenus*) in Finland: a preliminary report. *Ornis Fennica* **62**: 145-162.

Kovacs, G. & Vegvari, Z. (1999). Population size and habitat of the Aquatic Warbler *Acrocephalus paludicola* in Hungary. *Vogelwelt* **120**: 121-125.

Kozulin, A. & Krogulec (1999). Habitat selection of the Aquatic Warbler *Acrocephalus paludicola* in Poland: consequences for conservation of the breeding areas. *Vogelwelt* 120: 64-71.

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 Byelarussian mires. *Acta Ornithol*. **39**: 35-44.

Ktitorov, P., Bairlein F., & Dubinin, M. (2008). The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. *Landscape Ecology* **23**: 169-179

Leivits, A. & Vilbaste, H. (1990). Ulevaade roolindude randeuurimis programmi "Acroproject" töötulemustest 1987. aasta sügelsel. *Loodesevaatlus*i **988**: 105-124.

Lekve, K. Boulinier, T., Stenseth, N.C., Gjøæter, J., Fromentin, J.M., Hines, J.E., Nichols, J.D. (2002). Spatio-temporal dynamics of species richness in coastal fish communities. *Proceeding of the Royal Society of London* **269**: 1781-1789.

Leisler, B. (1985). Oko-ethologische voraussetzungen für die entwicklung von polygamie bei rohrsängern (Acrocephalus). *Journal für Ornithologie* **126**: 357-381.

Moore, F.R., Gauthreaux S.A., P Kerlinger, J.R. & Simons T.R. (1995). Habitat requirements during migration: important link in conservation In Finch D.M., Martin T.E. (eds.) *Management of Neotropical Migratory Birds*. Oxford University Press, US 512 pp.

Nichols, J.D, Boulinier, T., Hines, J.E., Pollock, K.H., Sauer, J.R. (1998). Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation Biology* **12**: 1390-1398.

Palmer, M.W. (1993). Putting things in even better order: the advantage of canonical correspondence analysis. *Ecology* **74**: 2215-2230.

Pavoine, S. & Dolédec, S. 2005. The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. *Environmental and Ecological Statistics* 12: 125–138

Rguibi Idrissi, H., Lefebvre G. & Poulin, B. (2004). Diet of Reed Warblers (*Acrocephalus scirpaceus*) at two stopovers sites in Moroco during autumn migration. *Revue d'Ecologie* **59**: 491-502.

Robbins, C.S. Sauer, J.R., Greenberg, R.G. & Droege S. (1989). Population declines in North American birds that migrate to the Neotropics *PNAS* **86**: 7658-7662

Roberts, M., (1985). The Spiders of Great Britain and Ireland, Vol. 1 & 2. Harley Books, Colchester, Essex.

Russell, R.W., Carpenter, F.L. Hixon, M.A., Paton, D.C. (1994). The Impact of Variation in Stopover Habitat Quality on Migrant Rufous Hummingbirds. *Conservation Biology* **8**: 483–490

Schaefer, H.M., Naef-Daenzer, B., Leisler, B., Schmidt, V., Müller, J.K. & Schulze-Hagen, K. (2000). Spatial behaviour in the Aquatic Warbler (Acrocephalus paludicola) during mating and breeding. *Journal für Ornithologie* **141**: 418-424.

Schmidt, M.H., Lefbvre, G., Poulin, B. & Tscharntke, T. (2005). Reed cutting affect arthropod communities, potentially reducing food for passerines birds. *Biological Conservation* **121**: 157-166.

Selmi, S., Boulinier, T. (2003). Does time of season influence bird species number determined from point-count data? A capture-recapture approach. *Journal of Field Ornithology* **74**: 349-356.

Stenseth, N.C., Lekve, K., Gjøæter, J. (2002). modelling species richness controlled by community-intrinsic and community-extrinsic processes: coastal fish communities as an example. *Population Ecology* **44**: 165-178.

Schulze-Hagen, K. Flinks, H. & Dyrcz, A. (1989). Brutzeitliche beutewahl beim seggenrohränger *Acrocephalus paludicola*. *Journal für Ornithologie* **130**: 251-255.

Szövényi, G. (2002). Qualification of grassland habitat based on their Orthoptera assemblages in the Köszeg Mountains (W-Hungary). *Entomologia Experimentalis et Applicata* **104**: 159-163.

Ter Braak, C.J.F. (1986). Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167-1179.

LEGENDS:

Table 1: Number of faecal samples collected for each Warbler species

Table 2: Percentage of each arthropod group found in faeces samples

Table 3: Factors influencing relative mass gain, each variable was adjusted to the other variables.

Figure 1: Canonical Correspondence Analysis, Axis 1 (28%), Axis 2 (5%) ordination of preys in relation to Warbler species (ACROLA, Aquatic Warbler; ACRSCI, Reed Warbler; ACRSCH, Sedge Warbler). *AraInd*, Araneida indeterminate; *AraClu*, Araneida Clubionidae; *AraTet*, Araneida Tetragnathidae; *ColInd*, Coleoptera indeterminate; *ColAlt*, Coleoptera Altisidae; *ColCar*, Coleoptera Carabidae; *ColCur* Coleoptera Curculionidae; *DipInd*, Diptera Indeterminate; *DipDol*, Diptera Dolichopodidae; *DipSyr*, Diptera Syrphidae; *HetInd*, Heteroptera indeterminate Heteroptera; *HetHyd*, Hydrometra stagnatorum; *HomAph*, Homoptera Aphid; *HomCic*, Homoptère Cicadelloidae; *HymInd*, Hymenoptera indeterminate; *hymChr*, Hymenoptera Chrysidae; *HymIch*, Hymenoptera Ichneumonidae; *LepInd*, Lepidoptera indeterminate**;** *ZygIsc* Odonata Coenagrionidae; *OrtCon*, Orthoptera *Conocephalus discolor*;

Figure 2: Variation of spiders families abundance in Aquatic Warbler faeces and three invertebrate sampling methods.

Figure 3: Variation of abundance of the main Aquatic Warbler preys categories among the three main habitats (A: blow trap, B: sweep net, errors bars represent standard errors, abundance of Diptera have been divided by a factor 5 in order to clarify the figure).

Figure 4: Mass gain strategies of the Reed Warbler (A), the Sedge Warblers (B) and the Aquatic Warbler (C), during autumn stopover in Audierne Bay marshes. Adult measures are shown in black circles, juvenile in grey circles.

Table 1: Number of faecal samples collected for each Warbler species

		Aquatic Warbler	Sedge Warbler	Reed Warbler
2001	August	9	1	-
	September	-	1	-
2002	August	11	-	-
	September	12	-	-
2003	August	50	64	21
	September	11	3	2
2004	August	32	8	5
	September	3	1	-
Total		128	78	28

Table 2: Percentage of each arthropod group found in faeces samples, for each group of taxa percentage of biomass are given in brackets.

Taxa	CCA abbreviation	Aquatic Warbler n = 571	Sedge Warbler n = 1027	Reed Warbler N = 173
Opilinioda (*Leiobucnum sp*)		0,2	0	0,6
Araneida total		**13,8 (13)**	**3,3 (8)**	**5,8 (14)**
Araneida indeterminate	*AraInd*	10,3	2,1	4,0
Araneida Araneidae (*Larinoides cornutus*)		0,4	0	0
Araneida Clubionidae (*Clubiona sp.*)	*AraClu*	1,9	0,3	0,6
Araneida Lycosidae		0,2	0,1	0,6
Araneida Tetragnathidae (*Tetragnatha extensa*)	*AraTet*	1,1	0,6	0
Araneida cocoon		0	0,2	0,6
Coleoptera total		**5,8 (5)**	**3,1 (7)**	**4,0 (9)**
Coleoptera indeterminate	*ColInd*	2,3	2,1	3,5
Coleoptera Altisidae	*ColAlt*	1,4	0,3	0,1
Coleoptera Cantharidae		0,2	0	0
Coleoptera Carabidae	*ColCar*	1,1	0,1	0,6
Coleoptera Curculionidae		0,9	0,5	0,3
Coleoptera Histeridae		0	0,1	0
Diptera total		**37,5 (9)**	**16,6 (10)**	**53,8 (33)**
Diptera Indeterminate	*DipInd*	31,7	15,1	49,7
Diptera Dolichopodidae	*DipDol*	4,7	1,3	2,9
Diptera Syrphidae	*DipSyr*	0,7	0	0,6
Diptera Tipulidae		0,4	0,1	0
Diptera Nematocera		0	0,1	0,6
Diptera Brachycera		0	0,3	1,2
Heteroptera total		**1,8 (1)**	**3,1 (4)**	**2,3 (3)**
Heteroptera indeterminate	*HetInd*	1,1	0,1	2,3
Heteroptera (*Hydrometra stagnatorum*)	*HetHyd*	0,7	3,0	0
Homoptera total		**21,0 (6)**	**66,7 (48)**	**22,0 (16)**
Homoptera (*prob. Hyalopterus pruni*)	*HomAph*	18,6	66,6	21,4
Homoptère (Cicadelloidae)	*HomCic*	2,5	0,1	0,6
Hymenoptera total		**4,0 (2)**	**6,0 (8)**	**11,6 (15)**
Hymenoptera indeterminate	*HymInd*	2,8	5,1	6,9
Hymenoptera Chrysidae	*hymChr*	0,2	0,6	1,2

Hymenoptera Ichneumonidae	*HymIch*	1,1	0,4	1,7
Hymenoptera Formicidae		0	0	1,7
Lepidoptera total	***LepInd***	**4,7 (8)**	**0,1 (0)**	**0,6 (2)**
Odonata total		**8,4 (43)**	**0,9 (12)**	**0,6 (8)**
Odonata indeterminate	*ZygIsc*	1,8	0	0,6
Odonata (Coenagrionidae)	*ZygIsc*	3,0	0,5	0
Odonata (Coenagrionidae *Ischnura elegans*)	*ZygIsc*	3,7	0,4	0
Orthoptera total		**2,8 (13)**	**0,3 (3)**	**0 (0)**
Orthoptera (*Chorthipus sp*)		0,7	0	0
Orthoptera (*Conocephalus discolor*)	*OrtCon*	2,1	0,3	0

Table 3: Factors influencing relative mass gain, each variable was adjusted to the other variables.

	Aquatic Warbler	Sedge Warbler	Reed Warbler
correlation between mass gain and number of day after first capture	$F_{1,35}$ = 42.80 ; P < 0.0001	$F_{1,3501}$ = 1733.60 ; P < 0.0001	$F_{1,2709}$ = 0.10 ; P = 0.75
Influence of year on mass gain	$F_{12,35}$ = 1.48 ; P = 0.17	$F_{12,3501}$ = 4.82 ; P < 0.0001	$F_{14,2709}$ = 6.32 ; P < 0.001
Influence of age on mass gain	$F_{1,38}$ = 0.12 ; P = 0.72	$F_{1,3501}$ = 2.46 ; P = 0.12	$F_{1,2709}$ = 7.34 ; P = 0.007

Figure 1: Canonical Correspondence Analysis, Axis 1 (28%), Axis 2 (5%) ordination of preys in relation to Warbler species (ACROLA, Aquatic Warbler; ACRSCI, Reed Warbler; ACRSCH, Sedge Warbler). *AraInd,* Araneida indeterminate; *AraClu,* Araneida Clubionidae; *AraTet,* Araneida Tetragnathidae; *ColInd,* Coleoptera indeterminate; *ColAlt,* Coleoptera Altisidae; *ColCar,* Coleoptera Carabidae; *ColCur* Coleoptera Curculionidae; *DipInd,* Diptera Indeterminate; *DipDol,* Diptera Dolichopodidae; *DipSyr,* Diptera Syrphidae; *HetInd,* Heteroptera indeterminate Heteroptera; *HetHyd,* Hydrometra stagnatorum; *HomAph,* Homoptera Aphid; *HomCic,* Homoptère Cicadelloidae; *HymInd,* Hymenoptera indeterminate; *hymChr,* Hymenoptera Chrysidae; *HymIch,* Hymenoptera Ichneumonidae; *LepInd,* Lepidoptera indeterminate**;** *ZygIsc* Odonata Coenagrionidae; *OrtCon,* Orthoptera *Conocephalus discolor*;

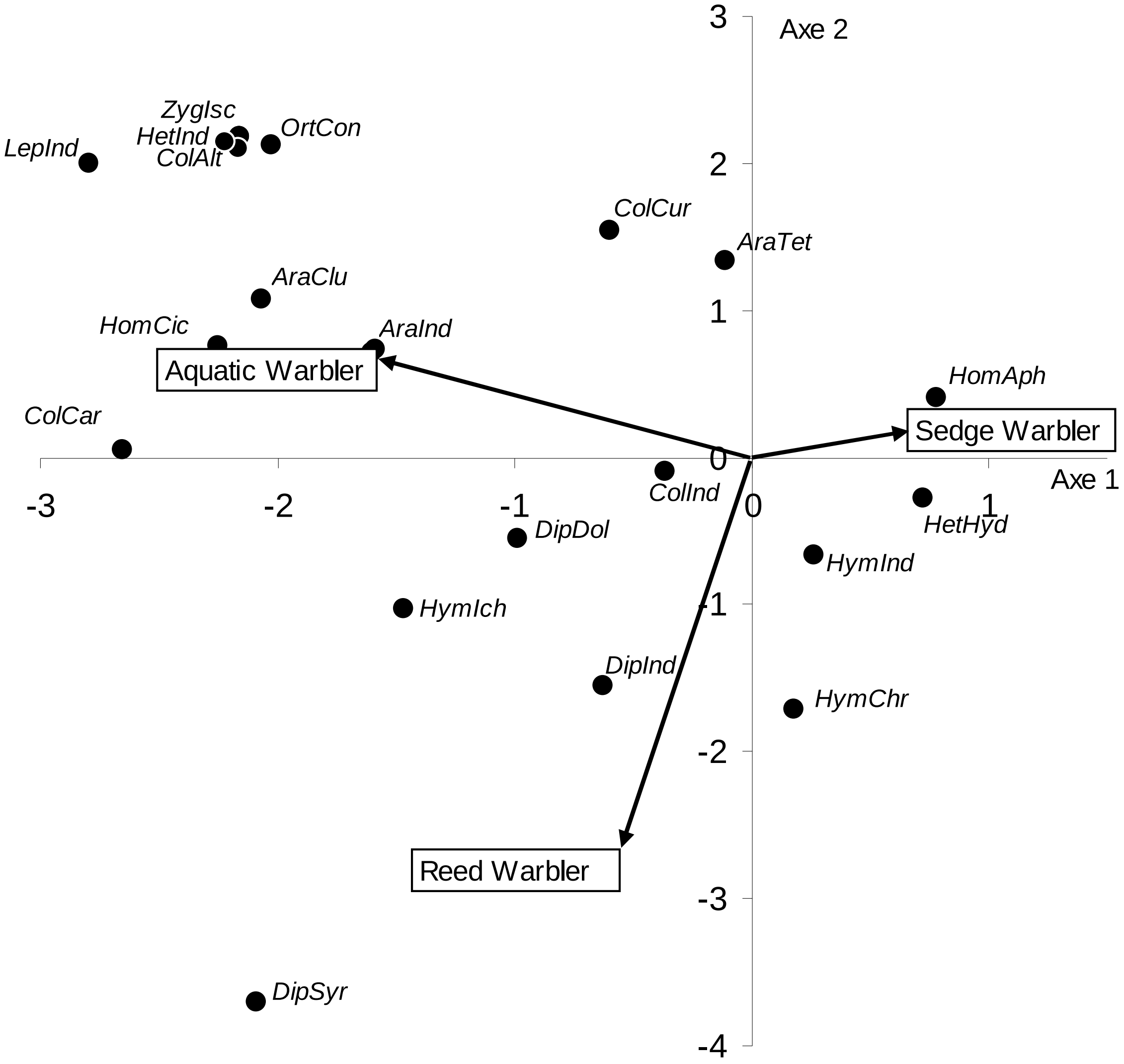

Figure 2: Variation of spiders families abundance in Aquatic Warbler faeces and three invertebrate sampling methods.

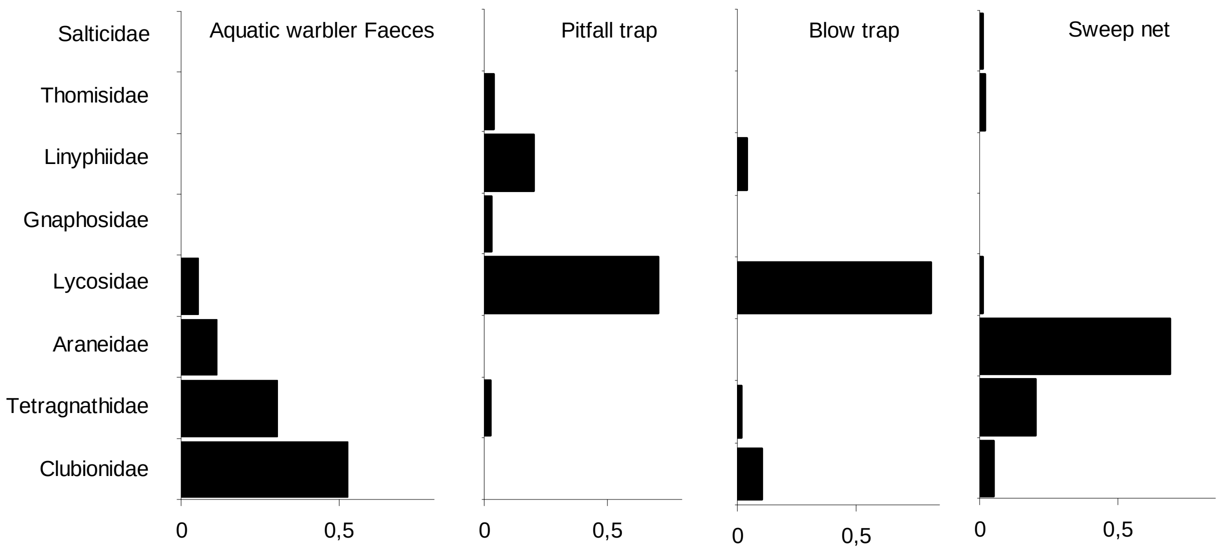

Figure 3: Variation of abundance of the main Aquatic Warbler preys categories among the three main habitats (A: blow trap, B: sweep net, errors bars represent standard errors, abundance of Diptera have been divided by a factor 5 in order to clarify the figure).

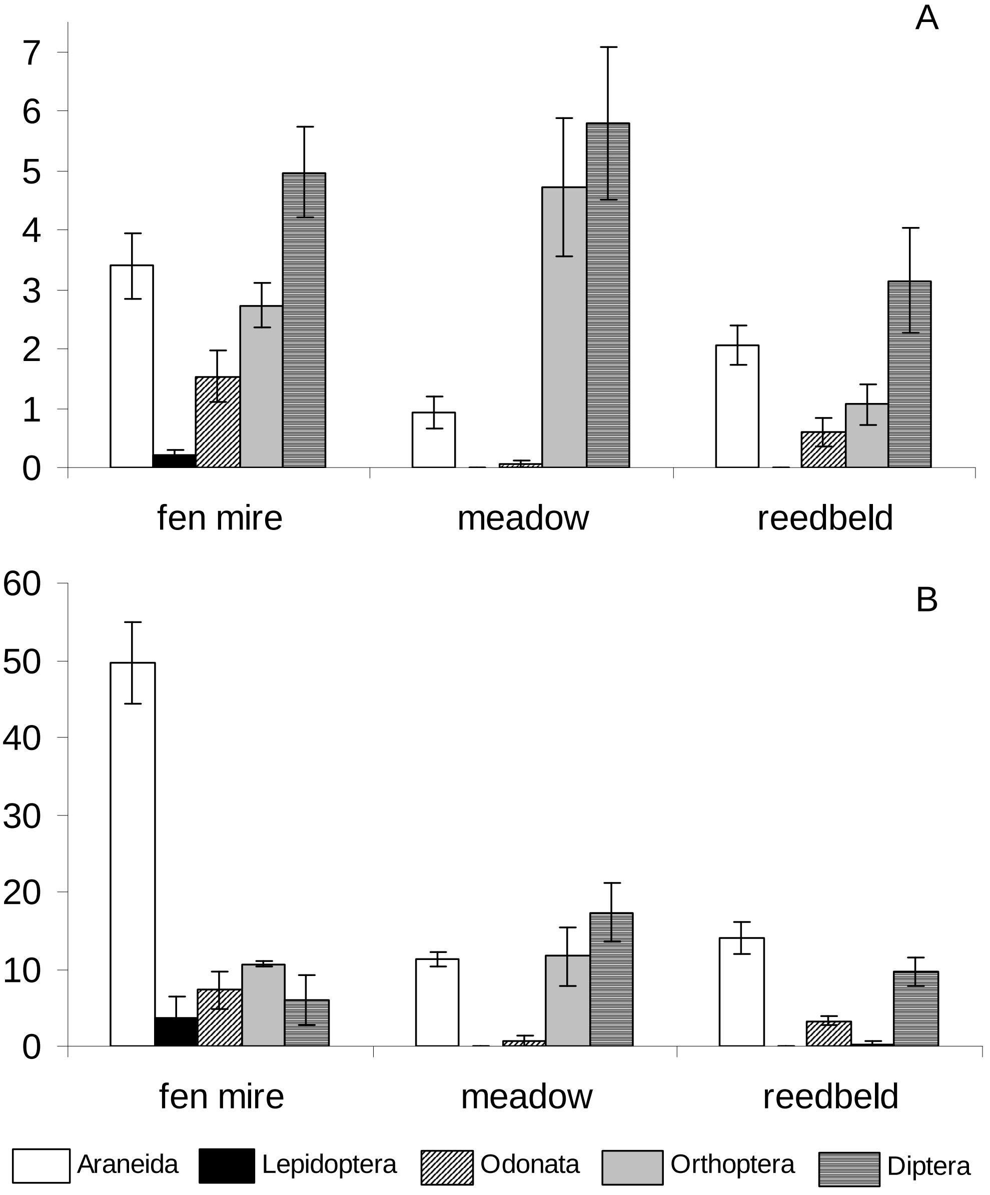

Figure 4: Mass gain strategies of the Reed Warbler (A), the Sedge Warblers (B) and the Aquatic Warbler (C), during autumn stopover in Audierne Bay marshes. Adult measures are shown in black circles, juvenile in grey circles. Mass in ordinate are expressed in relative mass gain (G') and in abscissa the number of days between two capture events.