DIET AND FUELLING OF THE GLOBALLY THREATENED AQUATIC WARBLER ACROCEPHALUS 1 PALUDICOLA AT AUTUMN MIGRATION STOPOVER AS COMPARED WITH TWO CONGENERS

Christian Kerbiriou, Bruno Bargain, Isabelle Le Viol, Sandrine Pavoine

To cite this version:

Christian Kerbiriou, Bruno Bargain, Isabelle Le Viol, Sandrine Pavoine. DIET AND FUELLING OF THE GLOBALLY THREATENED AQUATIC WARBLER ACROCEPHALUS 1 PALUDICOLA AT AUTUMN MIGRATION STOPOVER AS COMPARED WITH TWO CONGENERS. Animal Conservation, Wiley, 2011, 14 (3), pp.261-270. 10.1111/j.1469-1795.2010.00424.x . hal-02554674

HAL Id: hal-02554674
https://hal.archives-ouvertes.fr/hal-02554674

Submitted on 26 Apr 2020

DIET AND FUELLING OF THE GLOBALLY THREATENED AQUATIC WARBLER *ACROCEPHALUS PALUDICOLA* AT AUTUMN MIGRATION STOPOVER AS COMPARED WITH TWO CONGENERS.

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

[1] Muséum National d'Histoire Naturelle - UMR 7204 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 7204 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*

Word count:

SUMMARY

The effective conservation of aquatic warbler (*Acrocephalus paludicola*), one of the most threatened western Palaearctic migratory passerines, requires good knowledge of its ecological needs at stopover sites. In particular, identifying its diet, which controls the accumulation of fat reserves during migration, facilitates the selection and management of adequately protected areas. Further key information includes the relationship between prey species abundance and habitats of aquatic warbler on stopover. We performed standardised mist-netting in the Audierne marshes (western France) during 12 years, which resulted in the capture of 1,200 aquatic warblers, and provided measurements for mass gain and the collection of faeces to infer the birds' diet. Invertebrate sampling was carried out in the three main Audierne marsh habitats (reed bed, fen mire and meadow). In order to go beyond prey digestibility bias, we also studied two closely related *Acrocephalus* species, present at migration stopover sites during the same period. We found that the diet composition of aquatic warbler observed at migration stopover sites is based on large-sized prey (Odonata, Orthoptera, Lepidoptera). Like sedge warblers, aquatic warblers put on weight during migration stopovers (daily mass gain = 0.38g). This increase in weight suggests that the aquatic warblers might have adopted a strategy for long-distance migration with few stopovers only. Due to great differences in diet, conservation management for the threatened aquatic warbler at stopover sites should not rely on existing knowledge about sedge and reed warblers. Similarities in the diet of aquatic warbler between nesting areas and migration stopover areas and the relationship between habitat and prey abundance suggest that fen mires play an important role in the quality of the foraging habitat at stopover sites.

INTRODUCTION

A decline in long-distance migratory songbirds has been repeatedly observed. The causes of this decline are numerous: climate change (Both *et al.*, 2006), degradation of wintering, breeding habitats (Robbins *et al.*, 1989), or loss and fragmentation of stopover site (Huotto, 1998). Recently, the vital importance of the presence and quality of migration stopover sites to en route songbirds has come to the forefront of avian conservation (Petit, 2000). Long-distance migration requires exceptional reserves. Migratory songbirds must rest and deposit fat reserves in restricted stopover. There, the often high density of birds together with heavily depleted food supplies lead to a severe competition both within and among species (Newton, 2004). Accordingly, it is known that high-quality habitats at stopover sites and a preserved network of stopovers should be considered an essential component of strategies for the conservation of migratory bird populations (Ktitorov *et al.*, 2008, Newton, 2004). However, the quality value of a site may differ among species and the reserve managers need explicit recommendations.

The aquatic warbler (*Acrocephalus paludicola*) is a rare long-distance migratory bird species and is considered one of the most threatened western Palaearctic migratory passerines (Collar *et al.* 1994). Its populations suffered an important decline mainly due to the loss in their breeding habitat (Dyrcz & Zdunek, 1993; Kozulin *et al.*, 2004). In addition, like many insectivorous birds that breed in northern Europe and winter in sub-Saharan Africa, aquatic warbler crosses wide ecological barriers, which requires long uninterrupted flights fuelled by large fat deposits. The migration strategy includes departure date, flight duration, habitat and diet selection, and is known to be under considerable selection pressure (Bairlein & Totzke, 1992). Northern aquatic warbler populations migrate through western Europe in autumn, chiefly visiting marshes in the Netherlands, Belgium and western coastal regions of France. France hosts the largest number of individuals in migration (Julliard *et al.*, 2006). However, important, rapid losses in marsh areas have occurred on its migratory route: 50% of marsh areas in France were lost in the 1970-1990 period (Bernard 1994); 40% of freshwater wetlands were destroyed or degraded in the Netherlands in only a 10-year period (Holland *et al.*, 1995).

As highlighted in the European Action Plan (Heredia 1996), the effective conservation of these threatened migratory passerines requires a thorough description of its ecological needs at stopover sites. Yet, to the extent that we are aware, few studies have analysed aquatic warblers' diet, and these studies have focused on the breeding period only. Unfortunately, the ecological needs and the network of stopover sites of aquatic warbler cannot be derived from information on congeners, as species within the *Acrocephalus* genus can exhibit very different migration strategies (Bibby & Green, 1981). The direct observation of aquatic warbler feeding on stopover is hardly possible due to the rarity of this bird and to poor visibility in marsh habitats. In addition, indirect studies of diet through faeces analysis are hindered by differential prey digestibility between preys. To circumvent these difficulties, we chose to compare faeces of aquatic warbler and two more common congeners known to exhibit differential strategy (reed warbler, *Acrocephalus scirpaceus*, and sedge warbler, *Acrocephalus schoenobaenus*) within the same stopover area. This comparison revealed diet specificities of aquatic warbler with the underlying assumption that digestibility bias is equal among the three closely related species. We then identified the taxa that made a major contribution to the diet of each species and the taxa that distinguished the diet of aquatic warbler from the two other warblers. In addition, we studied the correlations between aquatic warbler's main prey and habitat.

The strategies that underpin long migratory distances differ among species. Some birds - such as reed warblers - are known to move in many short steps, others - like sedge warbler - negotiate the same distance in a few jumps with very long flights (Bibby & Green, 1981, Bensch & Nielsen, 1999). Consequently, physiological requirements and ecological and time constraints are different. Indeed, moving in a series of short flights requires smaller fat reserves on board. The comparison of mass gain during stopovers between aquatic, reed and sedge warblers is thus expected to inform us on strategies underlying long migratory distances. This information is of conservation concern because moving in a series of short flights requires many different suitable stopover sites en route. In this case, the removal of one site is less tragic, as these 'hoppers' can easily move to the next site. However, for species exhibiting long-haul flights, the disappearance or degradation of a critical stopover site would seriously impair migration.

METHODS

Focal species

Aquatic warbler is a globally threatened species (Collar *et al.*, 1994) whose breeding range shrank dramatically during the last decades. The species disappeared from its former breeding grounds in Austria, Belgium, France and the Netherlands (Bargain, 1999). The European population comprises 13,000 to 21,000 singing males, which were mostly 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 (Birdlife International, 2004).

Study area

The study was carried out in the Audierne marsh (western France, W4°19'14,0229 N47°55'15,0881). Three main vegetation types dominated the landscape from the coast to the inland: reed bed, fen mire and hygrophilous meadow. Reed beds surrounded the coastal lake and were dominated by common reed *Phragmites australis*; the water table was above ground level for most of the year. Fen mire comprised medium herbaceous vegetation (up to 1 m) and, in summer, the water table was only a few centimetres above ground level and sometimes dried up. Fen mires were dominated by numerous plant species including *Scirpus spp, Juncus ssp, Eleocharis spp*, *Iris pseudacorus*, *Oenanthe spp*. Hygrophilous meadows were grazed extensively and were dominated by *Agrostis spp* and *Dactylis glomerata*.

We performed standardised mist-netting between 1988 and 2006 (same mist-net type, localization and functioning period), which resulted in the capture of up to 60,000 sedge warblers, 26,000 reed warblers, and 1,200 aquatic warblers (for more details on the method used see Bargain *et al.*, 2002). Due to technical constraints, i.e. mist netting could not be set up in fen mires or meadows, we were only able to capture aquatic warbler on reed beds, however mist net were localized close to fen mire: less than 100 meters (for more detail on localization and habitat see Bargain *et al.*, 2002). The Audierne marsh is known as an important national breeding ground for reed warbler, whereas sedge warblers hardly ever breed in these marshes. However, sedge warblers that transit at the site during migration period represent 2% of the European breeding population (Bargain *et al.*, 2002). Moreover, this area is likely to constitute a major world stopover for aquatic warbler (Julliard *et al.*, 2006).

Faecal analysis

The diet of the three warblers was assessed by faecal analysis. Between 2001 and 2004, we collected 128, 78 and 28 samples of aquatic, sedge and reed warbler faeces respectively (with just one faecal sample by bird), during ringing operations in August and September. In order to collect faeces, we placed birds in special bags with a plastic-coated bottom, fifteen minutes before their release. Identifiable chitinous fragments were counted in each sample with the aim to estimate the minimum number of individuals of each taxonomic group (e.g. four Odonata wings were counted as one individual). This method likely led to some bias in diet evaluation, since soft-bodied or small preys are less readily detected. However, Davies (1977) demonstrated that there is a strong correlation between prey remains in the faeces and the composition of the true diet in other insectivorous passerines.

Identifying the specificity of the aquatic warbler's diet

We first conducted a Canonical Correspondence Analysis (CCA; Palmer, 1993) in order to evaluate the contribution of each prey species to the diet composition of aquatic, reed and sedge warblers. 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 evaluates (1) whether the diversity in diet composition was higher among faeces within warbler species than expected randomly (within-species diversity in diet composition) and (2) whether it was higher between faeces among warbler species than expected randomly (among-species diversity in diet composition). The significance of this hierarchy was tested using the permuting approach (n= 1000). Given that diet data mostly came from one month in one year (Table 1) we restricted these analyses (CCA and APQE) to August 2003 diet data, although similar results were obtained with the full data set.

Relationship between aquatic warbler's prey and habitat

To increase our knowledge on aquatic warbler's foraging habitat selection, we combined three semi-quantitative invertebrate sampling methods among the three major habitats of the Audierne marsh: (1) we made a pitfall trap, with unattractive conservative liquid, in order to assess invertebrate density-activity in the ground. However, as pitfall traps collected few of aquatic warblers' preys, they were not detailed in this study. (2) We used a yellow bowl trap for invertebrates collected in a medium level of vegetation (2 stations per habitat, 1 bowl trap per station, collection after 4 days of operation, total of 15 samplings per habitat). (3) We performed a standardised sweep-net in order to collect invertebrates in the upper part of the vegetation (2 samplings per habitat, walking a 25-m distance, done the same day for the 3 habitats). Variations in prey abundance among habitats were assessed using a Student's t-Test with p-values adjusted for multiple comparisons using Hochberg (1988) correction.

Comparing diet diversity of aquatic, sedge and reed warblers

We assessed prey richness within each warbler's diet, using faeces. Taking into account closeness in terms of phylogeny or mass, the fairly similar prey digestibility could be considered a robust assumption for the three warblers studied. However, equal detectability of all prey species is probably not met. For example, beetles are probably more detectable than Diptera. Hence, estimating diet richness using the classic cumulative curve approach is inappropriate. We therefore used statistical methods derived from capture-recapture approaches. However, instead of capturing individuals, we capture species; and instead of assessing population size, this approach provides an estimator of community size, here prey species richness. This method relies on a table with faeces samples as columns, species as rows and presence-absence as entries that constitutes the “capture histories matrix”. This approach models richness with heterogeneous species detection probabilities. Prey species richness was estimated with the jackknife estimator (Burnham & Overton, 1979). For more detail on methods see recent studies (Selmi & Boulinier, 2003; Lekve *et al.,* 2002; Kerbiriou *et al.,* 2007) addressing richness estimation and detection probabilities from species count data and using COMDYN software (Hines *et al.*, 1999). As reed warblers had the smallest faeces sample sizes, we performed 50 random re-samplings of faeces samples for each warbler to obtain identical sample sizes of faeces (n=10) (i.e. 50 “captures-histories” matrix constituted by 10 “captures” events) before the assessment of detectability and richness. Species richness between warblers was compared using Student's t-Test with p-values adjusted for multiple comparisons using Hochberg correction.

Comparing mass gain strategies during stopover

To compare mass gain strategies across the three warbler species, we analysed 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 (Bargain *et al.,* 2002). Whenever weather permitted, the ringing station was opened for a total of 77 effective days per year (SE±4 days; extreme: 44; 115). Each captured bird was ringed and when safety time between capture and release was not overtaking, birds were weighed and aged (two classes: adult and young, i.e. born within the year). When birds were captured several times within a day, we retained the first measure only. For each bird 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 the Audierne marshes, we collected a total of 6,724 body mass changes for sedge warbler, 6,470 for reed warbler and 47 for aquatic warbler. We used Generalised Linear Models (GLM, with *F* test in order to account for over-dispersion), to analyse whether body mass change was explained by the number of days between two capture events. Important factors are known to affect body mass of bird in migration such as age. Moreover we expect changes in mass during a day or over the seasons (Schaub & Jenni 2001). In addition, the mass gain of insectivorous bird could also vary across years due to great variations in prey availability. In order to limit biases due to variations in bird mass in the daytime, we only considered data from 7 to 11 am. Indeed, during this period we did not detect any significant difference between the time of capture and the time of recapture (respectively for the sedge, aquatic and reed warbler, $F_{1,2480}$=0.39, P=0.53 ; $F_{1,58}$=0.84 P=0.36 ; $F_{1,3150}$=2.59, P=0.11). In addition, there was no significant interaction between the day and the time of the day (respectively for the sedge, aquatic and reed warbler $F_{1,629}$=1.53, P=0.18 ; $F_{1,279}$=0.01, P=0.91 ; $F_{1,694}$=174.38, P=0.15). The other factors, age, season (i.e. day of the year), and year were included in GLM modelling with each variable tested adjusted to all the other variables.

As possible differences in mass gain are expected between birds with different mass, we used relative mass gain (*G'*) instead of gross mass gain to illustrate the relationship between mass change and stopover duration.

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

Mc is the mass measured during the first capture and *Mr* is the mass measured during the recapture. In order to cure heteroscedasticity in GLM analyses we log transformed *Mr* and *Mc*. In order to distinguish reed warbler breeders from migrants, we then used the same GLM analysis on birds for which the foreign origin was known (birds ringed during the breeding season in another country, n=23). For aquatic warbler, we used the entire national data in order to test the existence of regional differences in mass gain. Yet, complementary data came from Sandouville (W0°19'15 N49°29'51), Chenac-Saint-Seurin-d'Uzet (W0°49'58 N45°29'59) and Frossay-Le Massereau (W1°55'54 N47°14'41) where the same standardised mist-netting protocols were carried out.

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 1,731 prey items. In terms of prey abundance, the diets of aquatic and reed warblers were dominated by Diptera (38 and 54%, respectively) and aphids (21 and 22%, Table 2) whereas that of sedge warbler was dominated by aphids (67%), followed by Diptera (17%). Using a predictive model of the relationship between body length and invertebrate group mass (Ganihar, 1997), the contribution of Odonata, Araneida, Orthoptera, Diptera and Lepidoptera to consumed biomass was 43%, 13%, 12%, 9% and 8% respectively for aquatic warbler. For reed warblers, Diptera represented 33% of consumed biomass, aphids 16% and Hymenoptera 15%. For sedge warbler, aphids represented 48% of consumed biomass, Odonata 12%, and Diptera 10% (Table 2).

Taxa that underlined the specificity of aquatic warbler's diet, when considering abundance

The Canonical Correspondence Analysis (CCA) approach revealed that Lepidoptera, Araneida, Orthoptera, Odonata, Coleptera, Atlidae contributed to distinguishing the aquatic warbler's diet from that of the two other warblers (Fig.1). Aphids mainly contributed to the sedge warbler's diet while wasps and, to a lesser extent, flies contributed to the diet of reed warbler (Fig.1). These differences in diet composition among warbler species were significant, as shown by the APQE analysis ($P=0.001$), whereas no significant variation in composition was detected among faeces samples within warbler species ($P=0.91$).

Availability of aquatic warbler's prey among habitats.

The availability of the five principal preys in terms of biomass (Odonata, Orthoptera, Araneida, Lepidoptera and Diptera) varied across habitats (Fig. 2). The abundance of Araneida species was significantly higher in fen mires than in pasture ($P<0.001$ whatever the sampling method) or in reed beds ($P=0.04$ for bowl trap and $P<0.001$ for sweep net). The abundance of Odonata was higher in fen mires than in pasture ($P=0.002$ for bowl trap and $P=0.04$ for sweep net), but did not differ from reed beds ($P=0.06$ for bowl trap and $P=0.21$ for sweep net). Orthoptera abundance was high in both fen mires and pasture but no difference could be detected between the two habitats whatever the method used ($P=0.11$ and $P=0.71$ for bowl trap and sweep net, respectively). No significant difference was found between habitats for Diptera abundance ($P>0.20$ whatever the sampling method used). Lepidoptera (moth) were almost exclusively collected in fen mires.

Diet diversity of 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 sedge warbler faeces (13.2 preys; se=1.7) ($P<0.0001$). Yet, no significant difference was found between the number of preys of aquatic warbler and reed warbler (6.2 preys; se=0.8) ($P=0.52$).

According to the species richness estimate assessed with jackknife estimator, the aquatic warbler had a less diversified diet (16.9 species; se=1.3; on average in 10 faeces) than the other two warbler species (reed warbler: 22.2 species; se=2.5; sedge warbler: 28.8 species; se=4.6; P=0.02 and P=0.007 respectively). The average detection probability was generally high (0.77; se=0.07 for aquatic warbler, 0.72; se=0.02 for reed warbler and 0.72; se=0.04 for sedge warbler) and not significantly different across warbler species (GLM, $F_{2,147}$=1.58, P=0.20).

Finally, aquatic warblers consumed larger preys (average 9.2 mm; se=0.4) than reed (5.1mm; se=0.3; t value = 7.31, P<0.0001) and sedge warblers (4.6mm; se=0.3; t value = 4.57, P<0.0001).

Differences in mass gain strategies of aquatic, sedge and reed warblers during stopover.

Significant differences in mass between age classes were detected for the tree warbler studied: 10.99g se=0.02 for young and 12.02g se=0.06 for adult GLM, $F_{1,6709}$=448.44; P<0.0001 for sedge warbler; 10.97g se=0.01 for young and 11.20g se=0.03 for adult $F_{1,6195}$=112.83; P<0.0001 for reed warbler; 11.31g se=0.03 for young and 11.78g se=0.17 for adult $F_{1,1093}$=7.70; P=0.006 for aquatic warbler. The number of days between two capture events, significantly was influenced by the age class for sedge wabler ($F_{1,6709}$=15.92; P<0.0001) and reed warbler ($F_{1,6469}$=303.52; P<0.0001) but not for aquatic warbler ($F_{1,46}$=0.22; P=0.65).

Except for the estimate of mean daily mass gain and figure 3, all the analyses were carried out on relative mass gain (G’) with log transformation. No correlation between the relative mass gain and the number of days spent was detected for reed warbler (Table 3, Fig. 3). As there was probably a small proportion of local reed warbler breeders captured and recaptured that could have induced bias since they were not in migration behaviour (birds involved in late reproduction or in partial moult), we performed the same analysis on a subset of data including reed warblers known to be migrating due to foreign ring identities. Again, no correlation could be detected ($F_{1,20}$=2.51; P=0.13 and, moreover, the trend was slightly negative - 0,05g/days).

In contrast to reed warbler, the mass in sedge and aquatic warblers increased according to the number of days spent on the Audierne marshes migration stopover (Table 3, Fig.3). According to the linear regression between gross mass gain and time spent between capture and recapture, the mean daily mass gain was 0.21g se=0.01 for sedge warbler and 0.38g se=0.06 for aquatic warbler.

When all French data of aquatic warblers' mass gain are considered, no impact of year, season or age is detected ($F_{16,68}$=1.33; P=0.20; $F_{1,68}$=1.83; P=0.18 and $F_{1,68}$=0.31; P=0.57, respectively). In addition, no variation among the main sites where aquatic warblers were captured (Audierne marsh, Sandouville, Chenac-Saint-Seurin-d'Uzet and Frossay/Le Massereau) were detected ($F_{14,68}$=1.12; P=0.35). However, the same pattern of mass gain in relation to stopover duration as observed in Audierne is noted ($F_{1,68}$=6.59; P=0.01).

Mass gain varied significantly across the years for sedge and reed warblers (Table 3). Yet, there was no sign of unconditionally good or bad years, as yearly differences depended on the species: daily mass gain was significantly larger in 1993, 2000, 2003 and 2004 for sedge warbler, but significantly lower in 1991, 1994, 2000, 2002, 2003 and 2005 for reed warbler.

DISCUSSION

Diet specificity

The diet composition of aquatic warbler observed at the migration stopover sites of Audierne marshes is similar to that observed by Schulze-Hagen *et al*, (1989) in the species' breeding areas: the diet predominantly consists of Araneida, Diptera and Coleoptera (30%, 22% and 15% respectively in Schulze-Hagen's study and 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 prey: 9.2 mm at Audierne marshes vs. 8.4 mm (Schulze-Hagen *et al.*, 1989). Leisler (1985) found 12.1-mm prey sizes at breeding sites. The major difference between the Schulze-Hagen *et al.* study and ours is the presence of caterpillars in the former study, whereas none were detected here, which is probably due to the scarcity of such prey in late summer when aquatic warblers visit the stopover site. Although large prey species (Odonata, Araneida, Orthoptera) are found in small numbers (25% of total preys) in the aquatic warbler's diet, they significantly contribute to the total biomass consumed (68%). These three large prey groups only represented 23 and 20% of consumed biomass for sedge and reed warbler, respectively. Due to the potential differences in prey digestibility, the value of this result is mainly qualitative and the strength of the result lies in the comparison between warbler species. Accordingly, diet of aquatic warblers differs only slightly between the breeding and the migration period but its diet is definitely different from that of the two other warblers.

Similarly, the diet composition of sedge warbler estimated at the stopover site of Audierne marshes matched previous studies. The large contribution of aphids was already observed in the diet of sedge warblers in various breeding areas (Koskimies & Saurola, 1985 Leivits &

Vilbaste, 1990; Chernetsov & Manukyan, 2000) and on migration stopover (Bibby & Green, 1981). Furthermore, observed aphid outbreaks around the study site (Bargain *et al.*, 2002) are consistent with years of increased mass gain. However, a lot of alternative preys have been inventoried, (Chernetsov & Manukyan, 2000) including Diptera, Coleoptera, Hymenoptera, and Araneida, which is consistent with our results: among the three warbler species, the diet of sedge warbler presented the highest prey species richness estimate.

Reed warbler also exhibited a diverse diet, which was yet centred on Diptera and, to a lesser extent, Hymenoptera and aphids. This type of diet composition was also observed by Bibby & Green (1981), Evans (1989), Grim & Honza (1996), Grim (2006), Rguibi Idrissi *et al.* (2004). Once again, average prey size in the reed warbler's diet measured in this study (5.1 mm) was close to that observed by Leisler (1985), 5.4 mm, or Rguibi-Idrissi *et al.* (2004), 4.5 to 5.4 mm.

The major part of the prey biomass in the aquatic warbler's diet that was distinct from the diet of the two other warblers was recorded in fen mires rather than reed beds. Spider families found in the aquatic warbler's diet, such as *Clubionidae, Araneidae,* and *Tetragnatidae*, and the absence of Lycosidae or Gnaphosidae, indicated that aquatic warbler did not forage on the ground level of vegetation (according to the functional group requirements of the families described in literature; Duffey, 1962; Roberts, 1985; Marc & Canard, 1997).

Mass gain

In Audierne's marshes and three other French marshes, Aquatic warblers' mass gain strategies were very close to those of sedge warblers: they both exhibited a significant increase in body mass during their stopover, suggesting the accumulation of fat reserves. Sedge warblers, which migrate earlier and more rapidly than reed warblers, 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 (Bibby & Green, 1981, Bensch & Nielsen, 1999). Nevertheless, results from other stopover sites would be necessary to conclude that the aquatic warbler conducts a few-stop migration strategy as sedge warbler.

Conservation concerns

As regards the diet specificity of aquatic warbler, the choice and management of protected stopover areas for this species cannot only be based on existing knowledge on sedge and reed warblers. Moreover, according to the possible mass gain strategy and our initial knowledge on the stopover network of aquatic warbler (important refuelling and few migration stopovers), this species is thus expected to be more impacted by the degradation or loss of any important refuelling stopovers during migration. The current stopover known to be used by the aquatic warbler are thus of great importance for the conservation of this species. During the nesting period, the aquatic warbler is a habitat specialist species, preferring fen mires characterised by a mesotrophic level, a 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). As aquatic warbler are capture in reedbed certainly this vegetation plays a role for stopover, however our study underlined that higher abundance of several prey species occurs in fen mires. In addition, the first results found in France with radio-tagged birds in stopover migration also indicated that fen mires are very used by aquatic warblers (Provost *et al. in prep.*). This habitat plays an important role in allowing the complete life cycle of aquatic warbler's prey. Fen mire vegetation maximises the abundance of 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).

However fen mires in western European coast (i.e. the aquatic warbler migration route) are localized at the margin of reed beds due to hydrological constraints. The main threat for these small areas of fen mires is firstly direct human destruction such as drainage and agriculture (pasture or maize culture). A second threat is the encroachment of shrubs in marsh edge and reed vegetation of open wetlands (Kloskowski & Krogulec, 1999). In European Atlantic stopover sites, mostly comprising large areas of common reed, conservation measures should therefore aim at maintaining areas of medium vegetation height (50–100cm). Restoration management, such as clearing, should focus on marsh edges which are often colonised by shrub willow associated with common reed. However, reed cutting, especially cutting for commercial reasons, appears to affect the arthropod communities with, for instance, observed decreases in some passerine birds' prey, such as Coleoptera and Araneida, together with increases in other prey, such as aphids (Schmidt *et al.*, 2005). To minimise negative effects, reed cutting should be restricted to small areas, connected with uncut areas, thereby allowing arthropod recolonisation (Schmidt *et al.*, 2005). In addition, the creation of small ponds near reed beds is expected to provide habitat patches with exceptional densities of Diptera (Brunel *et al.*, 1998) and Odonata.

Acknowledgments

The mist-netting operation on the Audierne marsh was only made possible thanks to the help of many volunteers of the ‘Bretagne Vivante’ association, as well as volunteer bird ringers. Furthermore, we wish to thank P. Frebourg, G. Le Guillou, F. Baroteaux, Y. Beauvallet, O. Benoist, B. Caillaud, L. Demongin, B. Dumeige, P. Frebourg, P. Gautier, G. Goujon, C. Ingouf, G. Le Guillou, J. Pigeon, J. Pourreau, J. Pineau, P. Provost, ringers working for the Museum, who provided aquatic warbler data from other places than the Audierne marsh. Many thanks to Olivier Dehorter for the extraction of these data from the Museum ringing database. Finally, we thank Frédéric Jiguet, Romain Julliard, Jean-Pierre Moussus, Emmanuelle Porcher, Michael Schaub and two anonymous reviewers for providing us with sound advice on an earlier version of this manuscript. This study received financial support from the French Ministry of Ecology and the French National Centre for Scientific Research, and is part of the LIFE project ‘Conservation of the Aquatic Warbler in Brittany’, 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., 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.

Bensch, S. & Nielsen, B. (1999). Autumn Migration Speed of Juvenile Reed and Sedge Warblers in Relation to Date and Fat Loads. *Condor* **101**: 153-156.

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.

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. & 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.

Duffey, E. (1962). A Population Study of Spiders in Limestone Grassland. *Journal of Animal Ecology* **31**: 571-599

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. & Pollock, K.H. (2003). COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study* **46**: 209-217.

Hochberg, Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. Biometrika, **75**: 800-803.

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.

Hutto, R.L., (1998). On the importance of stopover sites to migrating birds. *Auk* **115**: 823-825

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* **88**: 715-728

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.

Marc, P. & Canard, A. (1997). Maintaining spider biodiversity in agroecosystems as a tool in pest control. *Agriculture, Ecosystems & Environment* **62** : 229-235.

Newton, I. (2004). Population limitation in migrants, *Ibis* **146**: 197-226

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

Petit, D.R., (2000). Habitat use by landbirds along nearctic-neotropical migration routes: implication for conservation of stopover habitats. *Studies in Avian Biology* **20**: 109-114.

Provost, P., Kerbiriou, C. & Jiguet, F. Foraging range size and habitat use of radio-tagged Aquatic Warblers during fall migration stopover *in prep*

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.

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.

Schaub, M. & Jenni, L. (2001). Stopover durations of three warbler species along their autumn migration route. *Oecologia* **128**: 217-227.

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.

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.

Table 1: Number of faecal samples collected for each Warbler species across months and years in Audierne marshes.

		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 of Aquatic, Sedge and Reed Warble. For each group of taxa, the percentages 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 that influenced the relative mass gain. Each variable tested was adjusted to the other variables.

	Aquatic Warbler	Sedge Warbler	Reed Warbler
Influence of number of days after first capture	$F_{1, 32} = 27.72$; $P < 0.0001$	$F_{1, 6689} = 2479.42$; $P < 0.0001$	$F_{1, 6450} = 0.11$; $P = 0.73$
Influence of year on mass gain	$F_{11, 32} = 1.32$; $P = 0.25$	$F_{17, 6689} = 11.97$; $P < 0.0001$	$F_{1, 6450} = 7.99$; $P < 0.0001$
Influence of season (day of the year)	$F_{1, 32} = 0.61$; $P = 0.44$	$F_{1, 6689} = 74.38$; $P < 0.0001$	$F_{1, 6450} = 77.38$; $P < 0.0001$
Influence of age on mass gain	$F_{1, 32} = 0.01$; $P = 0.91$	$F_{1, 6689} = 22.99$; $P < 0.0001$	$F_{1, 6450} = 0.02$; $P = 0.87$.

Figure 1: Specificity of each Warbler's diet assess using a Canonical Correspondence Analysis, ordination of preys [Axis 1 (28%), Axis 2 (5%)]. *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*;

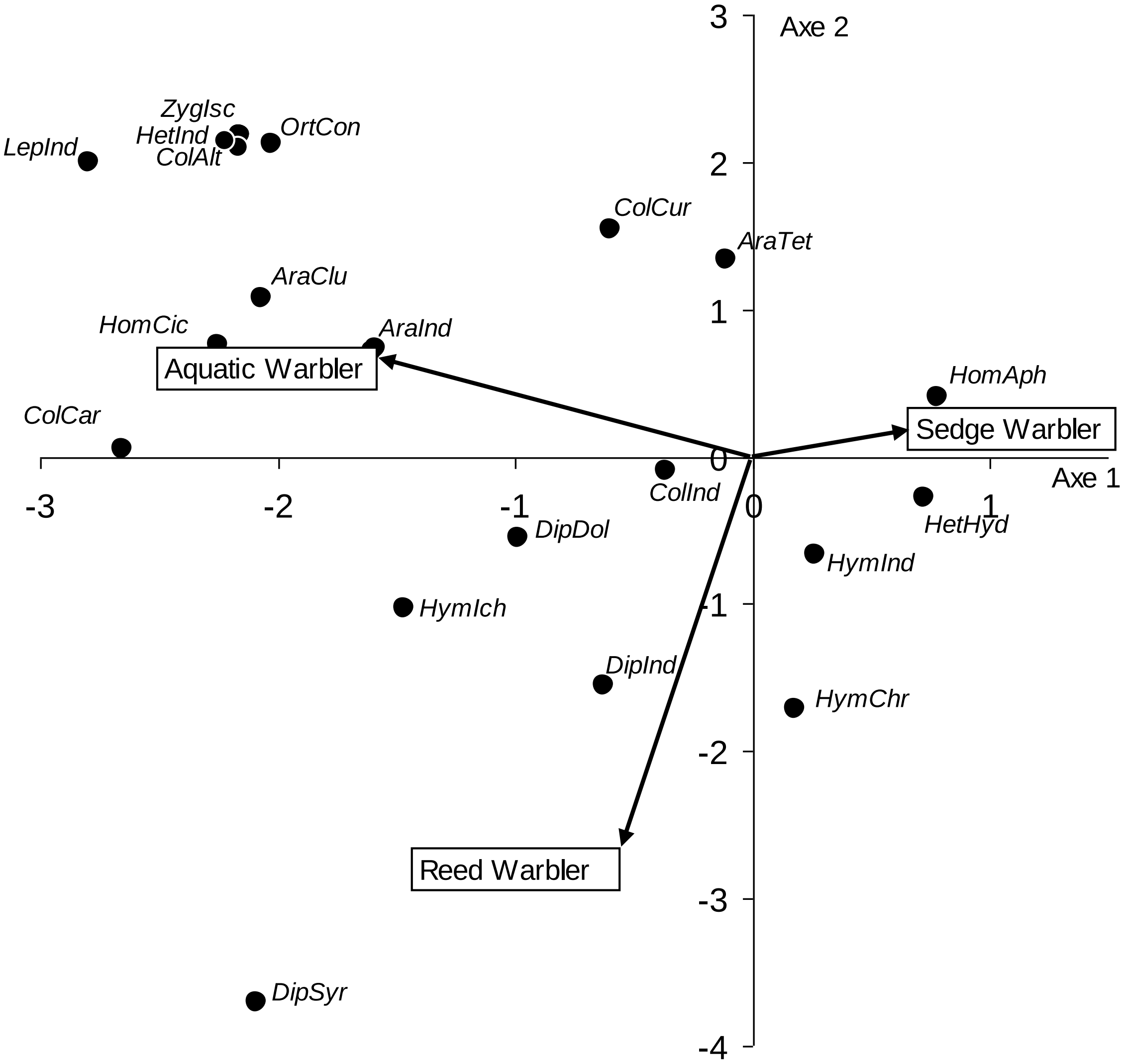

Figure 2: Variation of abundance of the main Aquatic Warbler prey categories among the three main habitats (units: number of individuals collected, A: bowl trap, B: sweep net, errors bars represent standard errors, left axis represent Diptera abundance).

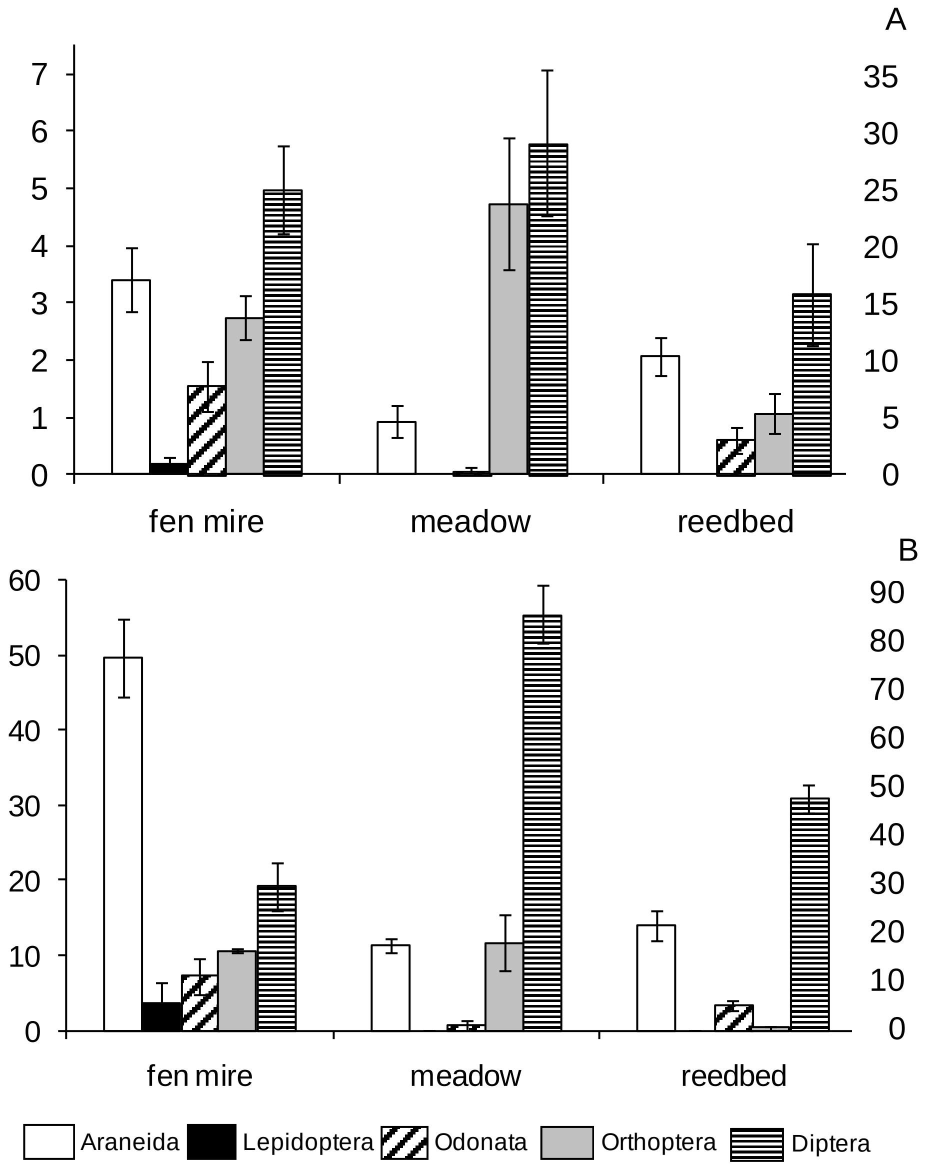

Figure 3: Mass gain strategies of the Reed Warbler (A), the Sedge Warblers (B) and the Aquatic Warbler (C), during autumn stopover in Audierne Bay marshes. Adult measures are shown in black circles, juvenile in grey circles. Mass in ordinate are expressed in relative mass gain (G') and in abscissa the number of days between two capture events.