

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

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

The effective conservation of aquatic warbler (Acrocephalus paludicola), one of the most 26 threatened western Palaearctic migratory passerines, requires good knowledge of its 27 28 ecological needs at stopover sites. In particular, identifying its diet, which controls the 29 accumulation of fat reserves during migration, facilitates the selection and management of 30 adequately protected areas. Further key information includes the relationship between prev 31 species abundance and habitats of aquatic warbler on stopover. We performed standardised 32 mist-netting in the Audierne marshes (western France) during 12 years, which resulted in the 33 capture of 1,200 aquatic warblers, and provided measurements for mass gain and the 34 collection of faeces to infer the birds' diet. Invertebrate sampling was carried out in the three 35 main Audierne marsh habitats (reed bed, fen mire and meadow). In order to go beyond prey 36 digestibility bias, we also studied two closely related Acrocephalus species, present at 37 migration stopover sites during the same period. We found that the diet composition of 38 aquatic warbler observed at migration stopover sites is based on large-sized prey (Odonata, 39 Orthoptera, Lepidoptera). Like sedge warblers, aquatic warblers put on weight during 40 migration stopovers (daily mass gain = 0.38g). This increase in weight suggests that the 41 aquatic warblers might have adopted a strategy for long-distance migration with few 42 stopovers only. Due to great differences in diet, conservation management for the threatened 43 aquatic warbler at stopover sites should not rely on existing knowledge about sedge and reed 44 warblers. Similarities in the diet of aquatic warbler between nesting areas and migration 45 stopover areas and the relationship between habitat and prey abundance suggest that fen mires 46 play an important role in the quality of the foraging habitat at stopover sites.

#### 48 INTRODUCTION

49 A decline in long-distance migratory songbirds has been repeatedly observed. The causes of 50 this decline are numerous: climate change (Both et al., 2006), degradation of wintering, 51 breeding habitats (Robbins et al., 1989), or loss and fragmentation of stopover site (Huotto, 52 1998). Recently, the vital importance of the presence and quality of migration stopover sites 53 to en route songbirds has come to the forefront of avian conservation (Petit, 2000). Long-54 distance migration requires exceptional reserves. Migratory songbirds must rest and deposit 55 fat reserves in restricted stopover. There, the often high density of birds together with heavily 56 depleted food supplies lead to a severe competition both within and among species (Newton, 57 2004). Accordingly, it is known that high-quality habitats at stopover sites and a preserved 58 network of stopovers should be considered an essential component of strategies for the 59 conservation of migratory bird populations (Ktitorov et al., 2008, Newton, 2004). However, 60 the quality value of a site may differ among species and the reserve managers need explicit 61 recommendations.

62 The aquatic warbler (Acrocephalus paludicola) is a rare long-distance migratory bird 63 species and is considered one of the most threatened western Palaearctic migratory passerines 64 (Collar et al. 1994). Its populations suffered an important decline mainly due to the loss in 65 their breeding habitat (Dyrcz & Zdunek, 1993; Kozulin et al., 2004). In addition, like many 66 insectivorous birds that breed in northern Europe and winter in sub-Saharan Africa, aquatic 67 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 68 69 diet selection, and is known to be under considerable selection pressure (Bairlein & Totzke, 70 1992). Northern aquatic warbler populations migrate through western Europe in autumn, 71 chiefly visiting marshes in the Netherlands, Belgium and western coastal regions of France. 72 France hosts the largest number of individuals in migration (Julliard *et al.*, 2006). However, 73 important, rapid losses in marsh areas have occurred on its migratory route: 50% of marsh 74 areas in France were lost in the 1970-1990 period (Bernard 1994); 40% of freshwater 75 wetlands were destroyed or degraded in the Netherlands in only a 10-year period (Holland et 76 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 82 information on congeners, as species within the Acrocephalus genus can exhibit very different 83 migration strategies (Bibby & Green, 1981). The direct observation of aquatic warbler feeding 84 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 85 86 differential prey digestibility between preys. To circumvent these difficulties, we chose to 87 compare faeces of aquatic warbler and two more common congeners known to exhibit 88 differential strategy (reed warbler, Acrocephalus scirpaceus, and sedge warbler, Acrocephalus 89 schoenobaenus) within the same stopover area. This comparison revealed diet specificities of 90 aquatic warbler with the underlying assumption that digestibility bias is equal among the three 91 closely related species. We then identified the taxa that made a major contribution to the diet 92 of each species and the taxa that distinguished the diet of aquatic warbler from the two other 93 warblers. In addition, we studied the correlations between aquatic warbler's main prey and 94 habitat.

95 The strategies that underpin long migratory distances differ among species. Some 96 birds - such as reed warblers - are known to move in many short steps, others - like sedge 97 warbler - negotiate the same distance in a few jumps with very long flights (Bibby & Green, 98 1981, Bensch & Nielsen, 1999). Consequently, physiological requirements and ecological and 99 time constraints are different. Indeed, moving in a series of short flights requires smaller fat 100 reserves on board. The comparison of mass gain during stopovers between aquatic, reed and 101 sedge warblers is thus expected to inform us on strategies underlying long migratory 102 distances. This information is of conservation concern because moving in a series of short 103 flights requires many different suitable stopover sites en route. In this case, the removal of 104 one site is less tragic, as these 'hoppers' can easily move to the next site. However, for species 105 exhibiting long-haul flights, the disappearance or degradation of a critical stopover site would 106 seriously impair migration.

107

#### 108 METHODS

#### 109 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 (BirdlifeInternational, 2004).

117

#### 118 Study area

119 The study was carried out in the Audierne marsh (western France, W4°19'14,0229 120 N47°55'15,0881). Three main vegetation types dominated the landscape from the coast to the 121 inland: reed bed, fen mire and hygrophilous meadow. Reed beds surrounded the coastal lake 122 and were dominated by common reed *Phragmites australis*; the water table was above ground 123 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 124 125 sometimes dried up. Fen mires were dominated by numerous plant species including Scirpus 126 spp, Juncus ssp, Eleocharis spp, Iris pseudacorus, Oenanthe spp. Hygrophilous meadows 127 were grazed extensively and were dominated by Agrostis spp and Dactylis glomerata.

128 We performed standardised mist-netting between 1988 and 2006 (same mist-net type, 129 localization and functioning period), which resulted in the capture of up to 60,000 sedge 130 warblers, 26,000 reed warblers, and 1,200 aquatic warblers (for more details on the method 131 used see Bargain et al., 2002). Due to technical constraints, i.e. mist netting could not be set 132 up in fen mires or meadows, we were only able to capture aquatic warbler on reed beds, 133 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 134 135 important national breeding ground for reed warbler, whereas sedge warblers hardly ever 136 breed in these marshes. However, sedge warblers that transit at the site during migration 137 period represent 2% of the European breeding population (Bargain et al., 2002). Moreover, 138 this area is likely to constitute a major world stopover for aquatic warbler (Julliard et al., 139 2006).

140

#### 141 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.

152

#### 153 Identifying the specificity of the aquatic warbler's diet

154 We first conducted a Canonical Correspondence Analysis (CCA; Palmer, 1993) in order to 155 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 156 157 analysis which allows diversity decomposition according to a given hierarchy (Pavoine & 158 Dolédec, 2005). Here, the hierarchy comes from Acrocephalus faeces and prey species in 159 each faeces. This analysis evaluates (1) whether the diversity in diet composition was higher 160 among faeces within warbler species than expected randomly (within-species diversity in diet 161 composition) and (2) whether it was higher between faeces among warbler species than 162 expected randomly (among-species diversity in diet composition). The significance of this 163 hierarchy was tested using the permuting approach (n=1000). Given that diet data mostly 164 came from one month in one year (Table 1) we restricted these analyses (CCA and APQE) to 165 August 2003 diet data, although similar results were obtained with the full data set.

166

#### 167 Relationship between aquatic warbler's prey and habitat

168 To increase our knowledge on aquatic warbler's foraging habitat selection, we combined three 169 semi-quantitative invertebrate sampling methods among the three major habitats of the 170 Audierne marsh: (1) we made a pitfall trap, with unattractive conservative liquid, in order to 171 assess invertebrate density-activity in the ground. However, as pitfall traps collected few of 172 aquatic warblers' preys, they were not detailed in this study. (2) We used a yellow bowl trap 173 for invertebrates collected in a medium level of vegetation (2 stations per habitat, 1 bowl trap 174 per station, collection after 4 days of operation, total of 15 samplings per habitat). (3) We 175 performed a standardised sweep-net in order to collect invertebrates in the upper part of the 176 vegetation (2 samplings per habitat, walking a 25-m distance, done the same day for the 3 177 habitats). Variations in prey abundance among habitats were assessed using a Student's t-Test 178 with p-values adjusted for multiple comparisons using Hochberg (1988) correction.

179

#### 180 **Comparing diet diversity of aquatic, sedge and reed warblers**

181 We assessed prey richness within each warbler's diet, using faeces. Taking into account 182 closeness in terms of phylogeny or mass, the fairly similar prey digestibility could be

183 considered a robust assumption for the three warblers studied. However, equal detectability 184 of all prey species is probably not met. For example, beetles are probably more detectable 185 than Diptera. Hence, estimating diet richness using the classic cumulative curve approach is 186 inappropriate. We therefore used statistical methods derived from capture-recapture 187 approaches. However, instead of capturing individuals, we capture species; and instead of 188 assessing population size, this approach provides an estimator of community size, here prev 189 species richness. This method relies on a table with faeces samples as columns, species as 190 rows and presence-absence as entries that constitutes the "capture histories matrix". This 191 approach models richness with heterogeneous species detection probabilities. Prey species 192 richness was estimated with the jackknife estimator (Burnham & Overton, 1979). For more 193 detail on methods see recent studies (Selmi & Boulinier, 2003; Lekve et al., 2002; Kerbiriou 194 et al., 2007) addressing richness estimation and detection probabilities from species count 195 data and using COMDYN software (Hines et al., 1999). As reed warblers had the smallest 196 faeces sample sizes, we performed 50 random re-samplings of faeces samples for each 197 warbler to obtain identical sample sizes of faeces (n=10) (i.e. 50 "captures-histories" matrix 198 constituted by 10 "captures" events) before the assessment of detectability and richness. 199 Species richness between warblers was compared using Student's t-Test with p-values 200 adjusted for multiple comparisons using Hochberg correction.

201

### 202 Comparing mass gain strategies during stopover

203 To compare mass gain strategies across the three warbler species, we analysed changes in 204 body mass between capture/recapture events within a same year and stopover site. Between 205 1988 and 2006, ringing operations were conducted, during the post-breeding migration 206 period: from early July to late September (Bargain et al., 2002). Whenever weather permitted, 207 the ringing station was opened for a total of 77 effective days per year (SE±4 days; extreme: 208 44; 115). Each captured bird was ringed and when safety time between capture and release 209 was not overtaking, birds were weighed and aged (two classes: adult and young, i.e. born 210 within the year). When birds were captured several times within a day, we retained the first 211 measure only. For each bird captured more than once, we recorded the change in body mass 212 between two capture events (the vast majority of individuals were recaptured only once, 213 which generated one data point per individual). At the Audierne marshes, we collected a total 214 of 6,724 body mass changes for sedge warbler, 6,470 for reed warbler and 47 for aquatic 215 warbler. We used Generalised Linear Models (GLM, with F test in order to account for over-216 dispersion), to analyse whether body mass change was explained by the number of days

217 between two capture events. Important factors are known to affect body mass of bird in 218 migration such as age. Moreover we expect changes in mass during a day or over the seasons 219 (Schaub & Jenni 2001). In addition, the mass gain of insectivorous bird could also vary across 220 years due to great variations in prey availability. In order to limit biases due to variations in 221 bird mass in the daytime, we only considered data from 7 to 11 am. Indeed, during this period 222 we did not detect any significant difference between the time of capture and the time of 223 recapture (respectively for the sedge, aquatic and reed warbler,  $F_{1,2480}=0.39$ , P=0.53; 224  $F_{1,58}=0.84$  P=0.36;  $F_{1,3150}=2.59$ , P=0.11). In addition, there was no significant interaction 225 between the day and the time of the day (respectively for the sedge, aquatic and reed warbler 226  $F_{1,629}=1.53$ , P=0.18;  $F_{1,279}=0.01$ , P=0.91;  $F_{1,694}=174.38$ , P=0.15). The other factors, age, 227 season (i.e. day of the year), and year were included in GLM modelling with each variable 228 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.

$$232 \qquad G' = \frac{(Mr - Mc)}{Mc}$$

233 Mc is the mass measured during the first capture and Mr is the mass measured during the 234 recapture. In order to cure heteroscedasticity in GLM analyses we log transformed Mr and 235 Mc. In order to distinguish reed warbler breeders from migrants, we then used the same GLM 236 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 237 238 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) 239 and Frossay-Le Massereau (W1°55'54 N47°14'41) where the same standardised mist-netting 240 241 protocols were carried out.

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243

#### 244 **RESULTS**

#### 245 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).

255

# Taxa that underlined the specificity of aquatic warbler's diet, when consideringabundance

- 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).
- 265

#### 266 Availability of aquatic warbler's prey among habitats.

- 267 The availability of the five principal preys in terms of biomass (Odonata, Orthoptera, 268 Araneida, Lepidoptera and Diptera) varied across habitats (Fig. 2). The abundance of 269 Araneida species was significantly higher in fen mires than in pasture (P < 0.001 whatever the 270 sampling method) or in reed beds (P=0.04 for bowl trap and P<0.001 for sweep net). The 271 abundance of Odonata was higher in fen mires than in pasture (P=0.002 for bowl trap and 272 P=0.04 for sweep net), but did not differ from reed beds (P=0.06 for bowl trap and P=0.21 for 273 sweep net). Orthoptera abundance was high in both fen mires and pasture but no difference 274 could be detected between the two habitats whatever the method used (P=0.11 and P=0.71 for 275 bowl trap and sweep net, respectively). No significant difference was found between habitats 276 for Diptera abundance (P>0.20 whatever the sampling method used). Lepidoptera (moth) 277 were almost exclusively collected in fen mires.
- 278

### 279 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).
- 294

#### 295 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).
- 303 Except for the estimate of mean daily mass gain and figure 3, all the analyses were carried out 304 on relative mass gain (G') with log transformation. No correlation between the relative mass 305 gain and the number of days spent was detected for reed warbler (Table 3, Fig. 3). As there 306 was probably a small proportion of local reed warbler breeders captured and recaptured that 307 could have induced bias since they were not in migration behaviour (birds involved in late 308 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 309 310 correlation could be detected ( $F_{1,20}=2.51$ ; P=0.13 and, moreover, the trend was slightly 311 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.

327

#### 328 **DISCUSSION**

#### 329 **Diet specificity**

330 The diet composition of aquatic warbler observed at the migration stopover sites of Audierne 331 marshes is similar to that observed by Schulze-Hagen et al, (1989) in the species' breeding 332 areas: the diet predominantly consists of Araneida, Diptera and Coleoptera (30%, 22% and 333 15% respectively in Schulze-Hagen's study and 14%, 38% and 6% in this study). Small 334 numbers of larger prey species such as Orthoptera, Lepidoptera, Odonata are also reported in 335 both studies. Both studies also concur on the average large size of prey: 9.2 mm at Audierne 336 marshes vs. 8.4 mm (Schulze-Hagen et al., 1989). Leisler (1985) found 12.1-mm prey sizes at 337 breeding sites. The major difference between the Schulze-Hagen et al. study and ours is the 338 presence of caterpillars in the former study, whereas none were detected here, which is 339 probably due to the scarcity of such prey in late summer when aquatic warblers visit the 340 stopover site. Although large prey species (Odonata, Araneida, Orthoptera) are found in small 341 numbers (25% of total preys) in the aquatic warbler's diet, they significantly contribute to the 342 total biomass consumed (68%). These three large prey groups only represented 23 and 20% of 343 consumed biomass for sedge and reed warbler, respectively. Due to the potential differences 344 in prey digestibility, the value of this result is mainly qualitative and the strength of the result 345 lies in the comparison between warbler species. Accordingly, diet of aquatic warblers differs 346 only slightly between the breeding and the migration period but its diet is definitely different 347 from that of the two other warblers.

348 Similarly, the diet composition of sedge warbler estimated at the stopover site of Audierne 349 marshes matched previous studies. The large contribution of aphids was already observed in 350 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).

370

#### 371 Mass gain

372 In Audierne's marshes and three other French marshes, Aquatic warblers' mass gain 373 strategies were very close to those of sedge warblers: they both exhibited a significant 374 increase in body mass during their stopover, suggesting the accumulation of fat reserves. 375 Sedge warblers, which migrate earlier and more rapidly than reed warblers, seem to 376 accumulate fat in northern France or southern England and fly almost directly to West Africa 377 over Iberia. In contrast, reed warblers migrate more slowly, thus over a longer period and 378 break up the journey by refuelling (Bibby & Green, 1981, Bensch & Nielsen, 1999). 379 Nevertheless, results from other stopover sites would be necessary to conclude that the 380 aquatic warbler conducts a few-stop migration strategy as sedge warbler.

381

#### 382 Conservation concerns

383 As regards the diet specificity of aquatic warbler, the choice and management of protected 384 stopover areas for this species cannot only be based on existing knowledge on sedge and reed 385 warblers. Moreover, according to the possible mass gain strategy and our initial knowledge on 386 the stopover network of aquatic warbler (important refuelling and few migration stopovers), 387 this species is thus expected to be more impacted by the degradation or loss of any important 388 refuelling stopovers during migration. The current stopover known to be used by the aquatic 389 warbler are thus of great importance for the conservation of this species. During the nesting 390 period, the aquatic warbler is a habitat specialist species, preferring fen mires characterised by 391 a mesotrophic level, a water table near the soil surface and intermediate vegetation height and 392 density (Kozulin & Flade, 1999; Kloskowski & Krogulec, 1999; Kovacs & Végvari, 1999; 393 Schaefer et al., 2000; Kozulin et al., 2004). As aquatic warbler are capture in reedbed 394 certainly this vegetation plays a role for stopover, however our study underlined that higher 395 abundance of several prey species occurs in fen mires. In addition, the first results found in 396 France with radio-tagged birds in stopover migration also indicated that fen mires are very 397 used by aquatic warblers (Provost et al. in prep.). This habitat plays an important role in 398 allowing the complete life cycle of aquatic warbler's prey. Fen mire vegetation maximises the 399 abundance of large Orthoptera prey Conocephalus discolor (Baldi & Kisbenedek, 1997; 400 Szövényi, 2002; this study) and the densities of Clubionidae and Tetragnathidae (Cattin et al., 401 2003; this study).

402 However fen mires in western European coast (i.e. the aquatic warbler migration 403 route) are localized at the margin of reed beds due to hydrological constraints. The main 404 threat for these small areas of fen mires is firstly direct human destruction such as drainage 405 and agriculture (pasture or maize culture). A second threat is the encroachment of shrubs in 406 marsh edge and reed vegetation of open wetlands (Kloskowski & Krogulec, 1999). In 407 European Atlantic stopover sites, mostly comprising large areas of common reed, 408 conservation measures should therefore aim at maintaining areas of medium vegetation height 409 (50–100cm). Restoration management, such as clearing, should focus on marsh edges which 410 are often colonised by shrub willow associated with common reed. However, reed cutting, 411 especially cutting for commercial reasons, appears to affect the arthropod communities with, 412 for instance, observed decreases in some passerine birds' prey, such as Coleoptera and 413 Araneida, together with increases in other prey, such as aphids (Schmidt et al., 2005). To 414 minimise negative effects, reed cutting should be restricted to small areas, connected with 415 uncut areas, thereby allowing arthropod recolonisation (Schmidt et al., 2005). In addition, the 416 creation of small ponds near reed beds is expected to provide habitat patches with exceptional 417 densities of Diptera (Brunel et al., 1998) and Odonata.

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

639Table 2: Percentage of each arthropod group found in faeces samples of Aquatic, Sedge and

640 Reed Warble. For each group of taxa, the percentages of biomass are given in brackets.

		Aquatic	Sedge	Reed
		Warbler	Warbler	Warbler
	CCA			
Таха	abbreviation	n = 571	n = 1027	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	Collnd	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	Hymlch	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	Zyglsc	1,8	0	0,6
Odonata (Coenagrionidae)	Zyglsc	3,0	0,5	0
Odonata (Coenagrionidae Ischnura elegans)	Zyglsc	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

- 643 Table 3: Factors that influenced the relative mass gain. Each variable tested was adjusted to
- 644 the other variables.
- 645

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

648 Figure 1: Specificity of each Warbler's diet assess using a Canonical Correspondence 649 Analysis, ordination of preys [Axis 1 (28%), Axis 2 (5%)]. AraInd, Araneida indeterminate; AraClu, Araneida Clubionidae; AraTet, Araneida Tetragnathidae; ColInd, Coleoptera 650 651 indeterminate; ColAlt, Coleoptera Altisidae; ColCar, Coleoptera Carabidae; ColCur 652 Coleoptera Curculionidae; DipInd, Diptera Indeterminate; DipDol, Diptera Dolichopodidae; 653 DipSyr, Diptera Syrphidae; HetInd, Heteroptera indeterminate Heteroptera; HetHyd, 654 Hydrometra stagnatorum; HomAph, Homoptera Aphid; HomCic, Homoptère Cicadelloidae; 655 *HymInd*, Hymenoptera indeterminate; *hymChr*, Hymenoptera Chrysidae; HymIch, Hymenoptera Ichneumonidae; LepInd, Lepidoptera indeterminate; ZygIsc 656 Odonata 657 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.



