



# Passerines use of maize crop in addition to reedbed in autumn: abundance, diet and food availability in anthropogenic wetland

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**Abstract** Wetland habitats experienced a dramatic reduction and fragmentation of biodiversity, because of human activities such as urbanization and agriculture. Now birds, as indicator of this biodiversity, have to breed, winter or stopover in wetlands embedded in a complex and highly altered human matrix. They may concentrate their activities in the wet remnant (wet reedbed) or suboptimal habitats (dry reedbed) and surroundings such as agricultural fields (maize). In a wide wetland area situated south-west of France in a main migration route, we tested if the abundance of passerine species differs among habitats according to their specialization and ecology (wet reedbed vs dry habitats; aquatics vs generalists; migrant vs local). We attempt to identify the underlying mechanisms of observed variation, looking at: arthropod availability

in each habitat, bird diet of five insectivorous species and refuelling capacity of birds. Maize crops hosted more invertebrates and biomass than reedbeds for Coleoptera, Diptera, Araneida and Cicadellidae. This may explain why crops were used by aquatic passerines (Bluethroat, Sedge warblers, Reed warblers), migrant or local generalists (Robin, Blue tit, Great tit, Willow Warblers and Nightingale). Bluethroat's diet was more focused on Formicidae and used the both habitats. In spite of the available food in maize, specialist birds preferred reedbed: Cetti warbler feeding in mainly Araneida and Cicadellidae; Sedge warbler Aphid and Coleoptera. Dry reedbed were better used by Grasshopper Warblers foraging Formicidae. Sedge and Reed warblers were more abundant in wet reedbed. We also noted for this last species young refuelling in maize crop. Therefore, the strategy to use maize crop may be different if resident or migrant. Generalist resident may disperse searching for food or transit area in continuity of vegetation; migrant need refuelling, particularly the aquatic trans-saharans more specialist on reedbed than the others. Finally, maize crop provided food resources and suitable shelter for a large group of species. It may be a supplement habitat of the wet and dry reedbeds, but not a substitute. Our study reaffirms to conserve and extend wet reedbed habitats threatened by clogging bush encroachment and drying.

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## Introduction

Anthropogenic land use is the major driver of habitat and biodiversity losses, mainly due to the agricultural and urban expansions: one third of the terrestrial land surface is now used for cropping or animal husbandry and urban area doubled since 1992 (IPBES 2019). One of the biological consequences of these increasing levels of human development is the large-scale decline of numerous birds' population, particularly insectivorous and specialist species (Bowler et al. 2019; Clavel et al. 2011) contributing to a homogenization of bird communities (Devictor et al. 2007; Le Viol et al. 2012). Agricultural intensification has affected farmland bird populations negatively (Donald et al. 2001; Stoate et al. 2001), declining them during the past half century in Europe (European Bird Census Council 2017) and in north America (Stanton et al. 2018). During the twentieth century, wetland habitats experienced also a dramatic reduction and an increased fragmentation, because of the pressure of human activities, such as urbanization and the drainage for agricultural use (Von Behren 2007; Whited et al. 2000; Czech and Parsons 2002). As a result, wetlands usually remain now embedded in a complex and highly altered human matrix, where many birds breed and/or use them as stopover sites during migration. In addition, many species may concentrate their activities in the wet habitats' remnants such as reedbeds, wet grasslands, fen mire, flooded bush.

Another aspect that has hitherto received little attention is the potential management and planning of the areas surrounding the wetland, such as pastured or cultivated lands. Some agricultural habitats may use as substitution, for example maize crop would have similar structure. These adjacent areas might be intensively used by migrants given the restricted size of wetland patches and the potential high intra and interspecific competition with other migratory and resident individual birds. This situation could be particularly exacerbated during the migration peaks, when large number of individuals can co-occur in a single location (Newton 2004). The challenge may be also critical for insectivorous and trans-saharian migratory birds who need to refuel for the long route, particularly before crossing a large barrier such as seas, mountains, or deserts (Alerstam and Lindström 1990; Delingat et al. 2008). Those circumstances predict that many migrants will be forced to use

alternative habitats out of the wetland. Many migrants that have specific breeding habitats will use a wider range of environments during migration (Petit 2000), but they are relatively understudied in this period in relation to other stages of the annual cycle (e.g. reproduction; Hutto 2000; Carlisle et al. 2009). Therefore, knowledge of the types of habitats and food resources used by migratory bird species at stopover sites need to be more investigated (Petit 2000; Schaub and Jenni 2001; Blount et al. 2021).

Although the migratory period poses separate challenges on birds than breeding and wintering, the consequences of farming practices and human activities for birds during migration need to be investigated. Some studies have been conducted during the migration period in farming landscape (Galle et al. 2009; Dänhardt et al. 2010, Roberston et al. 2011, Blount et al. 2021, Jorgensen et al. 2007). First results suggest croplands are mainly used by migratory generalist bird species, that can exploit a larger breadth of habitats (Blount et al. 2021), as well as species with preferences for habitats similar in structure to agricultural areas (Robertson et al. 2011; Fontanilles et al. 2020). So cultivated lands might be available habitats for migratory birds during migration. However, Blount et al. (2021) noted a lack of knowledge on birds' diet during migration, and showed no evidence that insectivorous birds prefer or avoid agricultural fields.

In this context, we investigated if highly altered wetlands that are interspersed in a maize crop matrix might be used by migrant and particularly insectivorous species. This possibility would be partly supported by the fact that maize crops have a similar vegetation structure to reedbeds. Only few studies have conducted research during the autumn or spring migration period in maize crops (Gottschalk and Cover 2016; Fontanilles et al. 2020; Wilcoxon et al. 2018; Galle et al. 2009; Jorgensen et al. 2007). Crop fields represent a large percentage of global land cover (Ramankutty and Foley 1999) and maize crop in South west of France is widespread and mature during the postnuptial migration period. In a previous study, we identified migrant Bluethroats *Luscinia svecica* select maize crops positively where invertebrates are present (Fontanilles et al. 2020). Bluethroat should be considered as an aquatic generalist species foraging in wet and dry habitats. Our hypothesis is that such generalist birds or non-aquatic species,

called here “terrestrial”, would have better capacities to use crop than specialists of wetlands, particularly insectivorous and aquatic migrants. This hypothesis needs to be checked also for specialist or generalist resident birds during the post-breeding period where adults and particularly young disperse exploring new habitats. We hypothesize young aquatic birds, less experimented, might use suboptimal habitats as maize crops, whereas more experimented adults, less dispersive, use optimal habitats as reedbeds and refuelling may be different (Piper 2011; Andueza et al. 2014; Newton 2004). We also hypothesize aquatic specialists in wetland habitats may not use crops where food and structure of the habitat should differ, while less specialised species should be more able to occur an exploit crop. Consequently, richness and diversity may be different in the two habitats, which can consequently affect the Community Specialization Index (CSI, Le Viol et al. 2012) may higher in reedbed.

In this study, we used a bird-ringing protocol to compare reedbeds and maize crops habitats in southwestern France, an area situated in a main migration route before crossing a mountain barrier (the western Pyrenees). We surveyed for two years during the autumn migration period two maize crops (with organic and not intense practice) and two types of reedbeds, one wet and the other dry during summer. We test if the abundance of species differs among habitat according to their specialization, and attempt to identify the underlying mechanisms of observed variation, looking at (i) arthropod availability in each habitat, (ii) bird diet of five insectivorous species, (iii) age-ratio, (iv) stopover duration, and (v) mass gain and fuel load of birds.

## Materials and methods

### Study area

We carried out our study in the Adour estuary, the “Barthes de la Nive” (West France, 43° 27' N; 01° 28' W), a site of 442 ha characterized by a mosaic of natural and agricultural habitats (Fig. A1 in Supplementary Material). Within this site some wetlands have been maintained safe from complete drainage due to its role in reducing the risk of flooding in Bayonne city. The wetlands are connected by channels to the Nive river, so some patches of wetland are

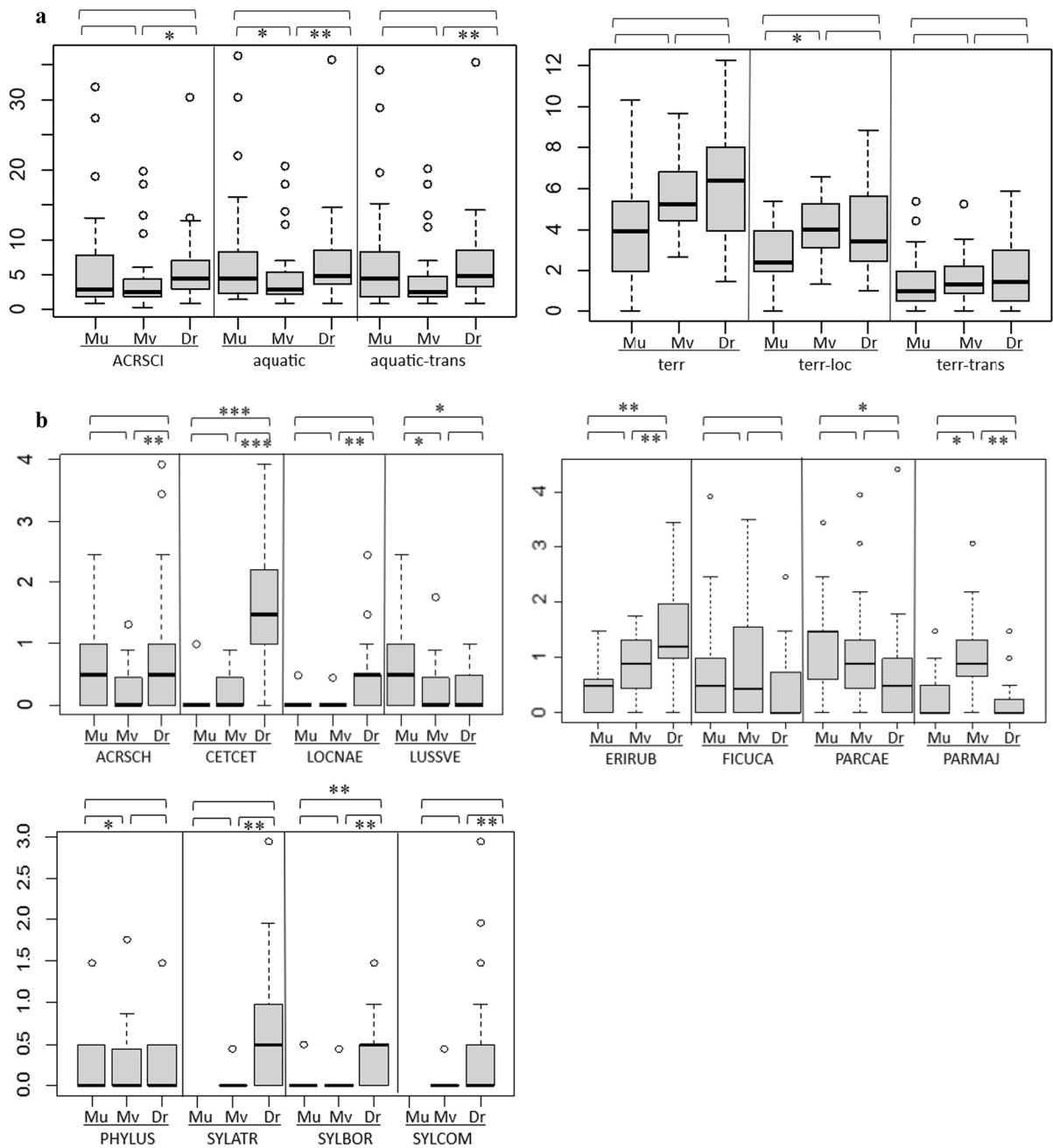
influenced by its flow, and the tidal regime. The site is a protected area included in the European Natura 2000 network (FR7200786), and is classified as Sensitive Natural Area by local authorities. Farming in the region uses a reasonably low quantity of fertilizers, herbicides and no insecticide. Isolated wetland patches are surrounded by agricultural areas, mainly maize crops (scattered in June and harvested after mid-September). We sampled two maize crops, one in Urdains (named MaizeU) the other in Villefranque (MaizeV); and two reedbeds, one in Urdains (wet-reedbed) the other in Villefranque (dry-reedbed). The wet-reedbed is cyclically flooded by tides, while the water level of the dry-reedbed is only determined by rainwater, particularly in winter and spring, but is normally dry during summer as maize crops.

### Difference in bird's species assemblage between reedbed and maize crop

Bird species can have specific habitat requirements for foraging and shelter. Species can be more prone to explore and use maize crops during their stopover periods, if they are migrants, or during their post-breeding season in the case of resident birds. Therefore, in this section, we estimated each species' preferences for reedbeds and maize crops by comparing their abundance and some stopover parameters (mass gain and stopover duration) in each habitat type.

*Bird data.* Data was obtained over two years between mid-august to mid-September, during the main migrating period of trans-saharian birds (Fontanilles et al. 2013). The MaizeV and reedbed sites were monitored in parallel in 2015 and, the two maize sites and the dry-reedbed in 2016. Only the dry-reedbed was monitored in 2016 because their dry soil water condition in summer was the same as maize fields, thus ensuring a better comparison with the two maize fields (Table 1). Birds were captured on mist-nets units (2 to 4 nets of 12 m × 2.5 m, 16 mm mesh) spread in the heart of the four sites to avoid edge effect. Mist-nets were opened for 5 h after dawn. Each captured bird was ringed, as individual identification is needed for assessing individual mass gain and stopover. Species, age and sex were determined and we measured wing length, and body mass following Demongin (2013).

With the aim to identify underlying mechanisms involve in habitat selection, we tested if species



**Fig. 1** Abundance index in 2016 in each site for species groups and species: trans (trans-saharian migratory species); aquatic (aquatic species); terr (terrestrial species); loc (local=resident); categories are defined in Table 6. Sites are Maize U (Mu), MaizeV (Mv), Dry-reedbed (Dr). The abundance index was the number of captures by 100 linear meters of mist nets/day/ha. The boxplots show the median (bold line), the first and third quartile as box, whiskers depict 1.5\*inter-

quartile range and outliers as points. The figures do not illustrate the dependant data linked by days for the three sites. Statistics comparisons of the abundance index of species and groups between sites were assessed by Wilcoxon test of paired days, p-values adjusted by the Holm method (see details in Suppl. information Appendix 4). Horizontal line up the graph represent test between two sites with significant p-values \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

**Table 1** Sampling period, linear meters of mist-nets, number of units in bracket (u) in each site and number of common sampling days between sites

Year	Period	Nb days		Maize sites		Reedbed sites			Number of common days							
				Villefranque		Urdaains		Villefranque		Urdaains						
				MaizeV	MaizeU	Dry-reedbed	Wet-reedbed	Dry-reedbed	Wet-reedbed	MaizeV-MaizeU	MaizeU-Dry-reedbed	MaizeU-Wet-reedbed	MaizeV-Dry-reedbed	MaizeV-Wet-reedbed	Reed-dry-reedbed	
2015	20–29/8;6/9;15–18/9	15		87 m (3u)		132 m (5u)	144 m (4u)						6	10	11	
2016	15/8–17/9	31		228 m (5u)	204 m (5u)	204 m (5u)		14	17	20						

segregate vertically in each habitat, using the five net-pockets (pocket 1 is the lowest one touching the ground and pocket 5 the highest just above the height of vegetation) where birds were captured in mist-nets as surrogate of height preference. Indeed, we expect the vertical structure may differ, specifically close to the ground, with a denser layer in reedbeds and a bare one in maize fields. This was done in the maize fields and the dry-reedbed from 5 to 17 on September in 2016. We compared the capture patterns in mist-net pockets for the main species according to a Wilcoxon 2-to-2 test, p-values adjusted by Holm's method.

#### Assemblage bird analysis

First, at each site, we determined the specific richness  $S$  (number of taxa), the diversity of the avifauna according to the Shannon index  $H'$  and the equitability  $E$  (Barbault 1995). We also calculated the Community Specialization Index (CSI, Le Viol et al. 2012) for each site and year, as the average Species Specialization Index to habitat (SSI, estimated in European range by Le Viol et al. 2012) of detected species weighted by their abundance within the sites' community (i.e., numbers of individuals by species) as follows:  $CSI = \text{sum}(a_i \times SSI_i) / \text{sum}(a_i)$ , where  $a_i$  is the abundance of species  $i$ .

Second, we checked whether the number of captures differed between the sites. For that, we defined the abundance index, number of captures by 100 linear meters of mist nets/day. In 2016, the mist-nets spatial distribution was constant (one unit/ha) but in 2015 it was not, so we also standardized by study area of each site (Minimum Convex Polygon area encompassing the units of each site): wet-reedbed 0.39 ha, dry-reedbed 1.51 ha and MaizeV 0.20 ha. The analysis was conducted for each species with sufficient sample per site and for the following groups: transsaharian migrants, resident birds, divided in aquatic and non-aquatic "terrestrial" species (see Table 5). The differences between sites were assessed by the Wilcoxon test of paired days, p-values adjusted by the Holm method. Day variable was a paired factor because the number of captures may vary greatly between days due to migration conditions (weather, decision to stopover).

### Age-ratio and stopover features

We assessed whether, for each species, age and sex ratios (for species determinable in the field) differed among sites. This was done by using Chi<sup>2</sup> tests. In case of low numbers, the two maize fields were combined. The number of days between the first and last capture was identified as an indicator of the stopover duration of individuals (Chernetsov 2012). However, note this is a minimum because individuals can be present before their first capture and after their last (Schaub et al. 2001). Similarly, we also calculated individual mass gain, as the difference of body mass between the first and last capture. We compared stopover duration and mass gain for some species with sufficient data in 2016, which was not the case for 2015. The fuel load is mainly stored in fat during the migration period (Salewski et al. 2009) and this influence body mass, with comparatively heavier individuals for their size having more fuel loads. To explore if fuel loads differ between sites/habitats, we run linear models for categories with more than 10 data per site, where body mass was used as dependent variable, and body size (wing length) were included as covariates. The analyses were performed with the 2016 dataset (the 2015 dataset was insufficient unless mentioned in the text).

### Structural difference and invertebrate availability between reedbed and maize crops

First, we described the spatial structure and invertebrate availability of the habitats that may influence choice of birds to use it.

#### Habitats sampling

The dry-reedbed site was a mixed reedbed, composed mainly of reed *Phragmites australis*, *Carex* species and bordered by maple *Acer negundo*. The wet-reedbed was a monospecific reedbed of *Phragmites australis*. Each one was bordered by willow *Salix sp.* Habitat structure was surveyed at the bird mist-net sampling (see Bird data) in each site: 3 replicates per mist-net spaced 4 m apart on each side alternately, one meter set back from the span. We noted the following measurements on a 50×50 cm square: number of green reeds/maize plants; the height and diameter of the green reed or maize plant that was

the closest to each corner of the square; the maximum height of other plants. In a circle of 50 m of radius around the center of each net, we evaluated by a global view average height and cover percentage of the herbaceous layer if present.

#### Invertebrate sampling

Arthropod availability has been linked to the post-breeding distribution of migratory birds (Moore et al. 1995; Bairlein et al. 1983; Roberston et al. 2011). We estimated the invertebrate availability between habitats. For this purpose, we assessed the variation in its abundance between the MaizeV and reedbeds. The MaizeU in the other bank of the Nive River had similar management practices, so it is expected to have a similar invertebrate availability. We applied two complementary approaches widely used in the estimation of arthropod availability (Graham et al. 2021) (i) pan-traps, including 3 standardized coloured (yellow, white, blue) bowl traps that allow to collect mainly flying insects; and (ii) pitfall glasses, (3 coloured bowls and a glass per station for a total of 12 stations, 6 in the maize crops, 3 in each reedbed) for focus the ground invertebrate communities. All stations were sampled simultaneously at 3 temporal stages in August 2015 and were deployed for four days. For more details, see Supplementary Material Ap. 3. For subsequent analyses, we pooled together the data of the three bowl traps of each station. We compared invertebrate availability, abundance and biomass between the two reedbeds and the maize crop using General Linear Models with a Poisson error distribution.

#### Diet of insectivorous birds

To try to elucidate why birds tend to use maize crop or reedbed, we analysed the invertebrate availability and diet of five insectivorous passerines: Sedge warbler *Acrocephalus schoenobaenus*, Reed warbler *Acrocephalus scirpaceus*, Cetti warbler *Cettia cetti*, Grasshopper warbler *Locustella naevia*, and Blue-throat *Luscinia svecica*. We collected 389 faecal samples during ringing operations for all sites. All remains identified in faeces were used to estimate the minimum number of prey items. While some bias in diet analyses was possible because small or soft-bodied preys are less easily detected, a strong correlation

has been found between prey remains in droppings and the actual composition of the diet (Davies 1977a; 1977b). We also assessed prey biomass using predictive models based on the relationship between body length and mass of terrestrial arthropods (Hodar 1996; see Supplementary Material Ap. 2 for additional details).

We conducted a canonical correspondence analysis (CCA) in order to evaluate the contribution of each prey species to the diet composition of the four birds. Only taxa representing more than 2% of the prey abundance were considered. We excluded Aphids from the analysis as it was only present in the Sedge warbler's diet structuring mainly the dataset and couldn't highlight other relationships and specific diet of other species in CCA (see figure with Aphids in appendix A2). Moreover, Aphids greatly fluctuated spatially and temporally. We tested the relationships by anova CCA, (library vegan R; Anderson and Willis 2003).

Unless specified, mean values are given  $\pm$  se (standard error). We used the R4.3.0 software (<http://cran.r-project.org>).

## Results

### Differences in species assemblages between reedbeds and maize crops

Bird richness was similar in both habitats, with 30 species identified, ranging from 22 to 30 depending on the site (Table 2). 10 to 14 species were trans-saharian migrants and 5 to 7 species were aquatic (Table 6). The diversity according to Shannon index is slightly higher in the reedbed than in the maize

crops according the year. The equitability is quite similar, with the dominance of Reed warbler in all sites (Table 6). The European SSI species ranged from 2.069 (*Prunella modularis*) to 6.892 (*Locustella luscinioides*) with more habitat specialists in the aquatic group (Table 6). The Community Specialization Index CSI seemed similar between sites, range [4.08; 5.62] in maize and [4.76; 5.10] in reedbed (Table 2).

### Birds' abundances

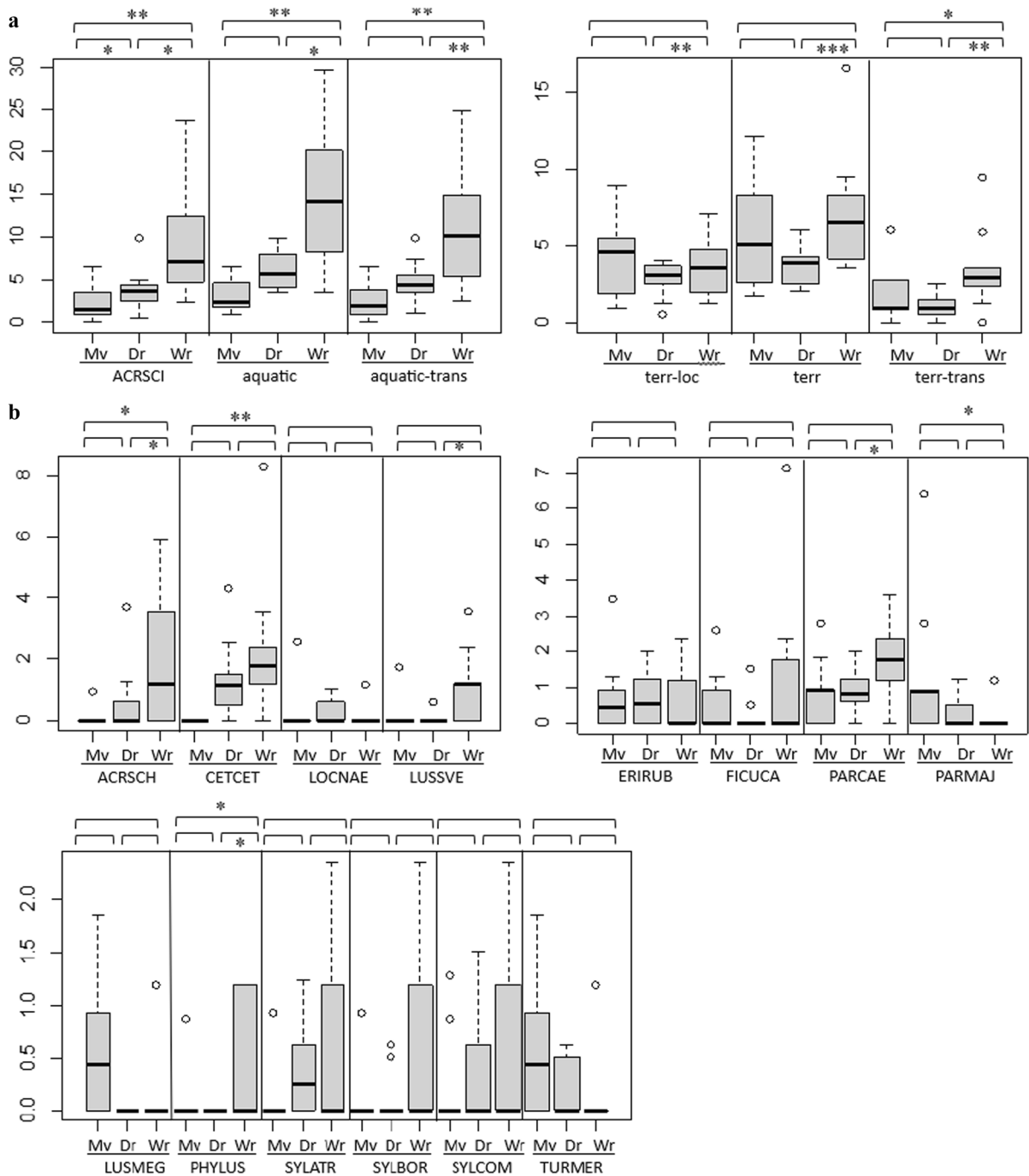
The aquatic group, and particularly trans-Saharan migrants, such as Reed warblers and Sedge warblers were more abundant in the wet reedbed (Fig 2a). They also exploit maize habitat as the dry reedbed (Figs. 1a and 2a). We had the same results for young and adult Reed warblers. Bluethroats, a short migrant and less specialist, could have similar abundance in maize crops as reedbeds. In contrast, the resident and specialist species Cetti's Warbler was more numerous in reedbeds than in maize fields (Figs. 1a and 2a). Grasshopper Warblers may be more abundant in the dry reedbed (in 2015 the population was too low, Fig. 2a).

Considering trans-saharian migratory terrestrial species, there were difference between the two habitats: the maize crops hosted as many Pied Flycatchers and Nightingales as the reedbeds; trans-saharian terrestrial species group and particularly Willow Warblers were more abundant in the wet-reedbed but not in the dry-reedbed (Figs. 1b and 2b). Garden Warbler and Common Whitethroat were also present in maize crops, although in smaller numbers than in the dry reedbed in 2016 (Fig. 1b).

**Table 2** Richness and diversity index per site

	2016				2015			
	MaizeU	MaizeV	total Maize	Dry-reedbed	Dry-reedbed	Wet-reedbed	total Reedbed	MaizeV
Richness (S)	22	27	30	30	18	24	26	22
Diversity H'	2.52	3.11	2.91	3.37	1.55	1.63	1.92	1.08
Hmax	4.46	4.75	4.91	4.91	4.17	4.58	4.70	4.46
Equitability	0.57	0.65	0.59	0.69	0.37	0.36	0.41	0.24
CSI	5.62	4.93	5.26	4.76	4.80	5.10	4.98	4.08
n	533	588	1121	830	191	286	477	94

n number of captures



**Fig. 2** Abundance index in 2015 in each site for species groups and species: trans (trans-saharian migratory species); aquatic (aquatic species); terr (terrestrial species); loc (local=resident); categories are defined in Table 6. Sites are MaizeV (Mv), Dry-reedbed (Dr), Wet-reedbed (Wr). The abundance index was the number of captures by 100 linear meters of mist nets/day/ha. The boxplots show the median (bold line), the first and third quartile as box, whiskers depict

1.5\*interquartile range and outliers as points. The figures do not illustrate the dependant data linked by days for the three sites. Statistics comparisons of the abundance index of species and groups between sites were assessed by Wilcoxon test of paired days, p-values adjusted by the Holm method (see details in Suppl. information Appendix 4). Horizontal line up the graph represent test between two sites with significant p-values \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$



For local or non-trans-saharian terrestrial species, maize fields might host more birds: Blue Tits in MaizeU or wet-reedbed, and Great Tit in MaizeV (Figs. 1b and 2b). We also noted Robins and Black-caps in maize fields, less abundant than in the dry reedbed in 2016 and similar in 2015.

Globally, we noted the importance of the wet-reedbed versus the dry habitats, dry-reedbed and maize crops, for the aquatic groups and particularly trans-Saharan migrants (Fig. 1a).

#### *Age-ratio and stopover features*

The ratio of juvenile Reed Warblers was higher in the dry reedbed than the combined maize (resp. 90% and 83.6%,  $\text{Chi}^2(1)=5.997$ ,  $p=0.014$ ); this proportion was higher in MaizeV (88.8%) than MaizeU (79.4%  $\text{Chi}^2(1)=8.041$ ,  $p=0.005$ ). Young Reed Warblers stayed on average 3.5 to 4.4 days with no difference between sites and habitat ( $W=2690$ ,  $p=0.26$ ). However, their mass gain was higher in maize crops (MaizeU  $+1.76 \pm 0.4$  g and MaizeV  $+0.68 \pm 0.2$  g) than in the dry reedbed ( $+0.4 \pm 0.1$  g;  $W=1854$ ,  $p=0.018$ ). Similarly, their fuel load was higher in the maize habitat ( $\beta = +0.29 \pm 0.1$  g  $t = -3.009$   $p < 0.01$ ). This difference was not significant in 2015 ( $\beta = -0.07 \pm 0.3$  g  $t = 0.238$   $p = 0.8$ ).

For the Pied Flycatcher, the fuel load was lower in reedbeds ( $\beta = -0.98 \pm 0.5$  g  $t = 2.006$   $p < 0.05$ ) and no significantly different for the other variables.

With regard to the Cetti's Warbler, no adults were captured in maize fields, which were more frequented by young males, and by females in reedbeds (sex ratio 0.67 vs. 0.29,  $\text{Chi}^2(1)=6.263$ ,  $p=0.012$ ). Blue Tits had a higher ratio of juveniles in maize fields, 84.2% vs. 62.5% in the dry Reedbed ( $\text{Chi}^2(1)=6.74$ ,  $p=0.009$ ) and their fuel load was lower ( $\beta = 0.25 \pm 0.1$  g  $t = -2.389$   $p < 0.05$ ). In 2015, juvenile Great Tits had a better body condition in MaizeV than reedbeds ( $\beta = 1.39 \pm 0.36$  g  $t = -3.898$   $p < 0.01$ ), which is not noted in 2016. No other significant differences in age, stopover duration and mass gain were observed for other species.

#### *Capture height*

In the maize fields, the Reed Warbler and Sedge Warbler were captured on average in pockets 3 and 4, higher than in the reedbed (Fig. 3, Reed Warbler

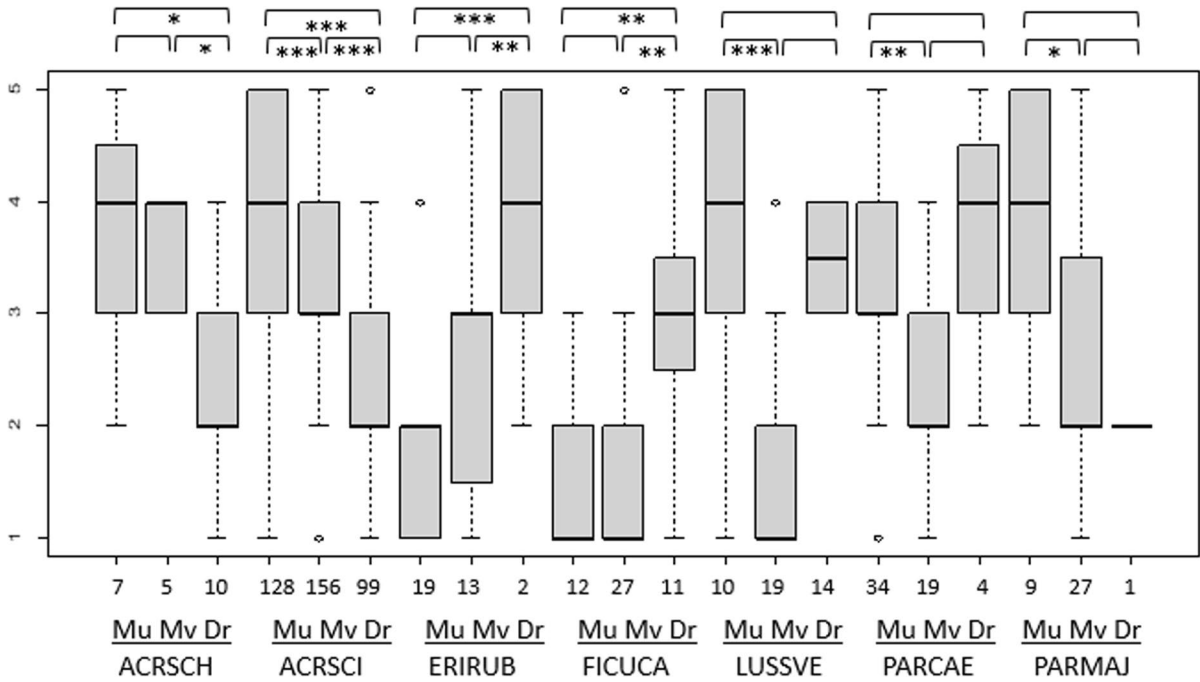
$W_{\text{MU/RV}}=11,043$   $W_{\text{MV/RV}}=11726$  all  $p < 0.0001$ ; Sedge Warbler  $W_{\text{MU/RV}}=59$   $W_{\text{MV/RV}}=44.5$  all  $p < 0.05$ ). Bluethroat was as frequent at the lower and upper parts of the maize fields ( $W_{\text{MU/RV}}=23.5$   $W_{\text{MV/RV}}=2.5$  all  $p > 0.05$ ).

Pied Flycatchers and Robins were caught lower in maize fields than in reedbed (Fig. 3 Pied Flycatchers  $W_{\text{MU/RV}}=15.5$   $W_{\text{MV/RV}}=59$  all  $p < 0.01$ ; Robins  $W_{\text{MU/RV}}=9.5$   $p < 0.001$   $W_{\text{MV/RV}}=56.5$  all  $p < 0.01$ ), indicating that they are closer to the ground. Blue Tit was captured at mid-height in the maize V and the Great Tit frequented the upper pockets in the maize U. Differences between sites for other species were not significant, often due to lower sample sizes.

#### **Structural differences between reedbed and maize crop**

The maize plants density was lower than reeds:  $2.83 \pm 0.1$  feet/0.25 m<sup>2</sup> on MaizeU and  $2.91 \pm 0.1$  on MaizeV (identical each other,  $z=0.128$   $p=0.8$ ) than in dry reedbed  $39.6 \pm 3.0$  ( $z=5.505$   $p < 0.0001$ ) and wet reedbed  $16.6 \pm 0.8$  ( $z=4.427$ ,  $p < 0.0001$ ). The heights of maize plants were intermediate to reeds (Fig. 4):  $2.70 \pm 0.3$  m MaizeV and  $2.96 \pm 0.47$  m for MaizeU ( $W=8989.5$ ,  $p < 0.0001$ ) were between  $2.02 \pm 0.03$  m for dry reedbed and  $3.35 \pm 0.05$  m for wet reedbed (higher  $t=22.1$ ,  $p < 0.0001$ ). On the other hand, diameters of maize plant were thicker (Fig. 5),  $19.9 \pm 0.54$  mm MaizeU and  $18.73 \pm 0.26$  mm MaizeV ( $W=7195.5$ ,  $p < 0.001$ ) against  $5.26 \pm 0.13$  mm for dry reedbed and  $9.01 \pm 0.11$  mm for wet reedbed ( $t = -26.547$   $p < 0.0001$ , different between reedbeds  $t = 21.68$   $p < 0.0001$ ).

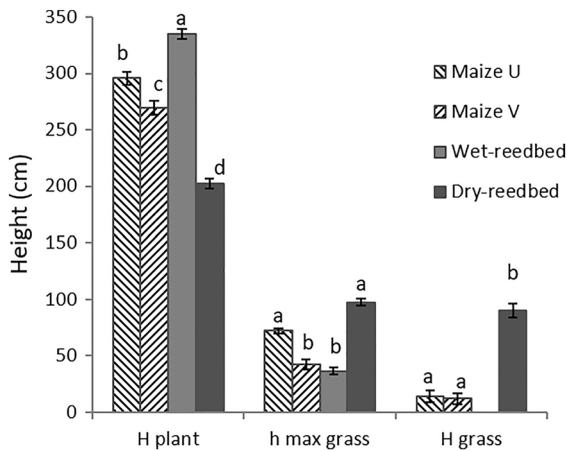
The grass layer was present in the maize fields and the dry reedbed, almost absent in the wet reedbed. Their cover was lower in maize than in dry reedbed: average  $6.2 \pm 1.5\%$  MaizeU,  $10 \pm 1.4\%$  MaizeV,  $13.23 \pm 0.8$  dry reedbed ( $W=28.5$ ,  $p=0.002$ , grouped maize). The average height of grass layer, identical to the two maize fields (MaizeU  $14 \pm 4.10$  cm and MaizeV  $12 \pm 3.03$  cm), was also lower than in dry reedbed  $106.8 \pm 6.28$  cm (Fig. 4,  $W=0$ ,  $p < 0.0003$ ). The maximum height of grass plants was also lower in MaizeV (mean  $42.2 \pm 4.4$  cm) than in dry reedbed ( $97.5 \pm 3.02$  cm,  $W=2192$ ,  $p < 0.01$ ) but not different from MaizeU ( $72.1 \pm 6.1$  cm,  $W=628$ ,  $p=0.3$ ,



**Fig. 3** Capture pocket in mistnet of species in the two maize crops (MaizeU Mu, MaizeV Mv) and the dry reedbed (Dr). Pocket 1 is the lowest one touching the ground and pocket 5 the highest just above the height of vegetation. The boxplots show the median (bold line), the first and third quartile as box, whiskers depict 1.5\*interquartile range and outliers as

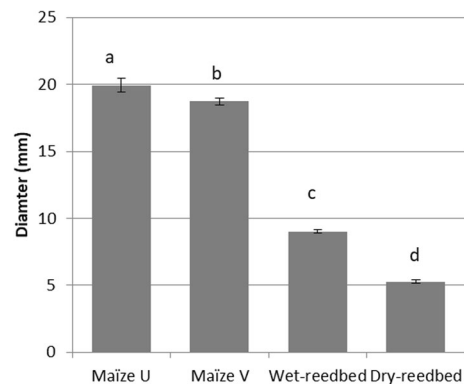
points. Statistics comparisons were assessed by Wilcoxon test, p-values adjusted by the Holm method. Horizontal line up the graph represent test between two sites with significant p-values \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . See Appendix 5 figure mean ( $\pm$  se) capture pocket in mistnet of species. The size of each sample is indicated on the x-label

**Fig. 4**). In conclusion, the structure of the two habitats was different, mainly on the aspects of density of



**Fig. 4** Height (mean  $\pm$  se) of reed and maize plants and other grass species for the tallest and the grass layer. Different letters represent significant p-values between sites, compared according to 2-to-2 test (Wilcoxon p-values adjusted by Holm’s method or t-test if normal distribution)

plants and cover of grass layer, which strongly affects structure.



**Fig. 5** Diameter of reed and maize plants. Different letters represent significant p-values between sites, compared according to 2-to-2 test (Wilcoxon p-values adjusted by Holm’s method or t-test if normal distribution)

### Diet analysis and habitat-specific invertebrate availability

In the 389 faecal samples, we recorded 1899 prey items. In terms of prey abundance, Araneida is the main prey contributing at least 20% of each bird's diet to 35.7% for Cetti warbler (Table 3). The diets of Sedge warbler were also dominated by Aphids (18.4%), Reed warbler by Coleoptera (22.3%), Cetti warbler by Cicadellidae (21.5%), Grasshopper warbler and Bluethroats by Formicidae (resp. 21.7% and 45.5% of their prey items).

Regarding the consumed biomass, Coleoptera was the major contributor at least 56%, maximum 71% for

Reed warbler. Secondary, Lepidoptera represented more than 8% by species, 27.5% for Grasshopper

**Table 4** Result of the anova CCA on diet specificity of the five insectivorous

	Df	ChiSquare	F	Pr(> F)
Reed Warbler	1	0.11322	19.9156	0.001
Bluethroat	1	0.13903	24.4555	0.001
Sedge Warbler	1	0.13903	24.4555	0.001
Cetti's Warbler	1	0.13434	23.6302	0.001
Grasshopper Warbler	1	0.01658	2.9172	0.012

**Table 3** Percentage of each arthropod group found in faecal samples of Sedge warbler *Acrocephalus schoenobaenus*, Reed warbler *Acrocephalus scirpaceus*, Cetti warbler *Cettia cetti*, Grasshopper warbler *Locustella naevia*, and Bluethroat *Luscinia svesica*.

Taxa	Sedge warbler	Reed warbler	Cetti warbler	Grasshopper warbler	Bluethroat
<i>Number of preys</i>	549	562	297	60	431
Arachnida Acarina	0 (0)	0 (0)	0 (0)	0 (0)	0.9 (0)
Arachnida Araneida	20.4 (8.4)	21.1 (7.6)	35.7 (16.9)	23.3 (8.1)	20.4 (13.4)
Coleoptera total	16.6 (60.6)	22.3 (71.1)	13.5 (56.7)	18.3 (56.7)	10.2 (59.6)
Coleoptera indeterminate	8.2	8.3	8.1	15.0	10.0
Coleoptera Alticinae	5.3	6.2	3.0	3.3	0.2
Coleoptera Curculionidae	2.0	3.2	1.3	0.0	0.0
Coleoptera Carabidae	1.1	3.2	0.7	0.0	0.0
Coleoptera Coccinellidae Anisosticta	0.0	1.1	0.0	0.0	0.0
Coleoptera Staphylinidae	0.0	0.2	0.3	0.0	0.0
Diptera total	11.5 (2.1)	13.5 (2.1)	14.8 (3.1)	6.7 (1)	7.4 (2.2)
Diptera indeterminate	10.2	12.2	13.1	6.7	6.5
Diptera Dolichopodidae	1.1	1.1	1.7	0.0	0.5
Diptera Nematocera	0.0	0.2	0.0	0.0	0.2
Heteroptera total	0.4 (0.1)	0.2 (0)	0.3 (0.1)	0 (0)	0.7 (0.2)
Hemiptera total	30.2	12.2	21.5	8.3	3.2
Hemiptera Cicadellidae	12 (5.1)	12.2 (4.5)	21.5 (10.5)	8.3 (3)	3.2 (2.2)
Hemiptera Aphidoidea	18.4 (2.9)	0 (0)	0 (0)	0 (0)	0 (0)
Hymenoptera total	14.0	26.4	9.8	30.0	49.9
Hymenoptera Formicidae	6.6 (0.7)	15.6 (1.4)	4.7 (0.6)	21.7 (1.9)	45.5 (7.5)
Hymenoptera No Formicidae	1.1 (0.7)	3.9 (2.1)	2.7 (1.9)	0 (0)	4.4 (4.3)
Hymenoptera indeterminate	6.4	6.9	2.4	8.3	3.0
Lepidoptera	5.8 (18.9)	3.9 (11)	2.4 (8.8)	10 (27.5)	1.6 (8.4)
Odonata	0.0	0.0	0.0	0.0	0.2
Neuroptera Myrmeleontidae Fourmilion	0.0	0.0	0.0	0.0	1.2
Crustacea Isopoda	1.1 (0.7)	0.4 (0.2)	2 (1.4)	3.3 (1.7)	2.3 (2.2)
Crustacea Malacostraca Amphipoda	0.0	0.0	0.0	0.0	0.2
<i>Gasteropoda</i>	0.0	0.0	0.0	0.0	1.6

For each group of taxa, the percentages of biomass are given in brackets

warbler. Cicadellidae contributed at 10.5% of the Cetti warbler's biomass diet.

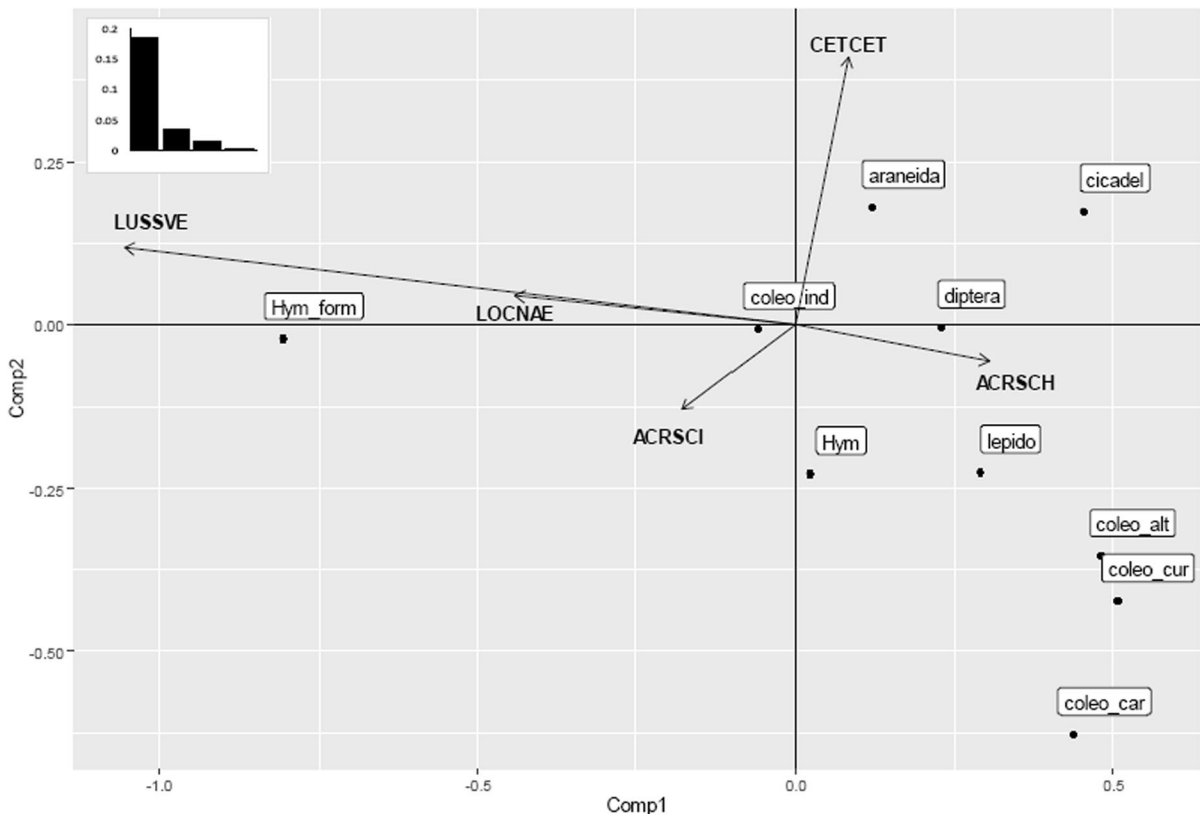
CCA analysis was significant ( $\text{Chi}^2(4)=0.23391$ ,  $F=10.286$ ,  $\text{Pr}( > F)=0.001$ , Table 4, see appendix A2 with Hemiptera Aphid include in CCA). Formicidae contributed mainly to the Bluethroat and Grasshopper warbler's diet, Araneidae and Cicadellidae to Cetti warbler, Coleoptera to Sedge warbler (Fig. 6).

Maize crops hosted significantly more invertebrates and biomass than reedbeds for beetles (Coleoptera), flies (Diptera) and spiders in pitfalls, and for leafhoppers (Cicadellidae) in bowls (Table 5). Maize crops also had higher availability of non-Formicidae hymenopterans than wet reedbed in bowls, but less than dry reedbed. Ants were more abundant in wet reedbed than in the other two sites, but they were concentrated in the dry part (where pitfalls were

put), while we hypothesise that in the other sites, they probably were more spread out (Table 5).

## Discussion

We inventoried similar bird richness (30) in August and September in maize and in reedbed, as other similar studies recorded (e.g. Gottschalk and Cover 2016). Generalist and terrestrial birds were more abundant in maize; whereas aquatic or specialist species preferred reedbed habitats. We discuss now these findings in relation to food availability and avian species ecology (i.e. diet, migratory behaviour and degree of specialization).



**Fig. 6** Diet specificity of the five insectivorous birds assess using a CCA (Canonical Correspondence Analysis), ordination of prey. ACRSCH: *Acrocephalus schoenobaenus*, ACRSCI=*Acrocephalus scirpaceus*, CETCET=*Cettia cetti*, LUSSVE=*Luscinia svecica*, LOCNAE=*Locustella naevia*. Prey abbreviations: coleo\_ind, Coleoptera indeterminate;

coleo\_alt, Coleoptera Altisidae; coleo\_car, Coleoptera Carabidae; coleo\_cur, Coleoptera Curculionidae; Hym, Hymenoptera indeterminate or No Formicidae; Hym\_form, Hymenoptera Formicidae; lepido, Lepidoptera; cicadel, Hemiptera Cicadellidae

**Table 5** Abundance and biomass (mean  $\pm$  SE) of arthropod groups in maize, dry reedbed and wet reedbed

Order	Family	Trap	Abundance			Biomass (mg)		
			Maize	Wet-reedbed	Dry-reedbed	Maize	Wet-reedbed	Dry-reedbed
Hymenoptera	Formicidae	Pitfall	0.2 $\pm$ 0.1	<b>1.1 <math>\pm</math> 0.3*</b>	0.2 $\pm$ 0.1	0.04 $\pm$ 0.02	<b>0.6 <math>\pm</math> 0.2 /Maize*</b>	0.2 $\pm$ 0.1
		Bowl	0.3 $\pm$ 0.1	–	0.6 $\pm$ 0.2	0.03 $\pm$ 0.02	0 $\pm$ 0	0.2 $\pm$ 0.1
Arachnida	Araneidae	Pitfall	3.5 $\pm$ 1**	0.8 $\pm$ 0.3	1.3 $\pm$ 0.4	<b>7.5 <math>\pm</math> 2*</b>	2.5 $\pm$ 1	4.8 $\pm$ 2.3
		Bowl	1.9 $\pm$ 0.4	1.2 $\pm$ 0.5	2 $\pm$ 0.6	3.4 $\pm$ 0.8	5.9 $\pm$ 2.9	<b>9.4 <math>\pm</math> 3.7**</b>
Coleoptera		Pitfall		0.1 $\pm$ 0.1	2.1 $\pm$ 0.5	<b>2006.9 <math>\pm</math> 449.1***</b>	1.9 $\pm$ 1.8	12.4 $\pm$ 4.2
		Bowl	<b>5.5 <math>\pm</math> 1.4***</b>	0.7 $\pm$ 0.3	3.8 $\pm$ 1.1***	<b>49.2 <math>\pm</math> 40.7***</b>	0.9 $\pm$ 0.6	8.2 $\pm$ 3.7
Diptera		Pitfall	<b>10.3 <math>\pm</math> 5.1***</b>	0.3 $\pm$ 0.2	1.1 $\pm$ 0.3	17.9 $\pm$ 7.1***	0.8 $\pm$ 0.8	1.1 $\pm$ 0.5
		Bowl	<b>24.5 <math>\pm</math> 6***</b>	1.4 $\pm$ 0.5	12.3 $\pm$ 2.5	42.2 $\pm$ 8.8***	1.8 $\pm$ 0.7	24.1 $\pm$ 5
Hymenoptera	non- Formicidae	Pitfall	0.9 $\pm$ 0.3	0.2 $\pm$ 0.1	<b>1.4 <math>\pm</math> 0.5 /Wr*</b>	0.7 $\pm$ 0.3	0.1 $\pm$ 0.1	<b>2.7 <math>\pm</math> 1.3**</b>
		Bowl	4.5 $\pm$ 1	0.6 $\pm$ 0.4	<b>8.9 <math>\pm</math> 1.6***</b>	14.4 $\pm$ 4.5	1.2 $\pm$ 1.1	<b>43.6 <math>\pm</math> 8.2***</b>
Hemiptera	Cicadellidae	Pitfall	0.3 $\pm$ 0.1	–	0.1 $\pm$ 0.1	0.2 $\pm$ 0.2	0 $\pm$ 0	0 $\pm$ 0
		Bowl	<b>2.7 <math>\pm</math> 0.7**</b>	0.1 $\pm$ 0.1	0.7 $\pm$ 0.3	<b>4 <math>\pm</math> 1.9 /Wr***</b>	0 $\pm$ 0	0.8 $\pm$ 0.4

They were trapped in pitfall and coloured bowls. We compared abundance and biomass between sites using General Linear Models with a Poisson error distribution. Numbers in bold indicate the site for which the abundance or biomass was significantly (\*\*p < 0.001; \*p < 0.01; \*p < 0.05) higher than one of the other sites (site shown after a slash symbol) or the other two sites. Two hyphens represent no data available

### Birds' diet and food availability in maize and reedbed

Maize crops hosted a lot of invertebrates and biomass. Cornouiller et al. (1997) showed also a relatively high insect abundance and biomass in maize crops. This could partly explain why the five bird species we studied could use this habitat. We detail below our interpretations for each of the five study species.

The Bluethroat appears to benefit by food availability in maize crops. Bluethroats typically forage on the ground (Orłowski et al. 2014; Allano et al. 1998; Cramp 2006) where ants, spiders and beetles are particularly abundant in maize. Moreover, the capture of Bluethroats in the upper parts of mist-nets could also reflect the exploitation of the Araneidae and Coleoptera that are available in the upper sections of the plants in both maize crops and reedbeds. Its diet fitted well with the trophic characterization made in other studies (Allano et al. 1998; Orłowski et al. 2014; Musseau et al. 2017). Bluethroats were more specialized on ants than the four other bird studied species.

Sedge warblers and Reed warblers fed more on Coleoptera and Diptera and also other various invertebrates (Araneida, Hemiptera, Lepidoptera, Heteroptera, Isopoda...), all included in previous studies (Chernetsov and Manukyan 1999; Kerbiriou et al. 2010; Idrissi 2004; Bibby and Green 1981). They were available in both habitats, probably in the leafy upper part of the plants where birds were more

frequently caught, particularly in maize crops. Aphids (Hemiptera) were only found in Sedge warbler's diet (18.4%). This insect group has been reported as the main food for this bird species during migration stopovers in reedbeds (67%; Kerbiriou et al. 2010; Bibby and Green 1981; Grandio 1998), which might contribute to explain the preference of Sedge warblers for reedbeds over maize crops. Nevertheless, this hypothesis could not be fully supported by our results because, although aphids only occurred in reedbeds, they were very rare during the study year and may fluctuate from year to year (only 2 aphids out of the 2400 counted arthropods). Aphids would need to be better studied by specific counts on leaves (Bibby and Green 1981) that we did not undertake in our study.

Grasshopper warbler used both habitats where it can forage on its favourite items, mainly Formicidae, Araneida and Coleoptera (Cramp 2006). This species was more abundant in the dry reedbed than maize crop in 2016; no significant difference was found in 2015, but its numbers were also lower. This species likes dense and dry vegetation foraging in low and ground parts, so that dry reedbed could fill better its habitat needs (Fontanilles et al. 2017).

In contrast to the four previous bird species, Cetti's Warbler diet cannot explain why it did not use maize crops. This species mainly feeds on Araneidae, Cicadellidae, and, less frequently, on Coleoptera or

**Table 6** Number of captures per species, per site in 2016 and 2015, Species Specialization Index (SSI), groups (trans = trans-saharian migrants, aqua = aquatic, terr = terrestrial, resid = resident species) and species codes

Species	code	Group	SSI	2016		2015		Dry-reedbed	Wet-reedbed
				MaizeU	MaizeV	MaizeU	MaizeV		
<i>Aquatic group</i>									
Reed Warbler	ACRSCI	<i>Aqua-Trans</i>	<b>6.892</b>	298	251	323	24	72	115
Cetti's Warbler	CETCET	<i>Aqua-Resid</i>	<b>3.933</b>	2	11	91		26	29
Sedge Warbler	ACRSCH	<i>Aqua-Trans</i>	<b>3.658</b>	25	13	45	1	10	27
Bluthroat	LUSOVE	<i>Aqua-Short</i>	3.377	28	16	11	4	1	13
Grasshopper Warbler	LOCNAE	<i>Aqua-Trans</i>	<b>3.907</b>	5	1	23	2	5	1
Great Reed Warbler	ACRARU	<i>Aqua-Trans</i>	<b>4.913</b>			1			
Savi's Warbler	LOCLUS	<i>Aqua-Trans</i>	<b>6.892</b>	1					1
Common Kingfisher	ALCATT	<i>Aqua-Short</i>	<b>5.687</b>				1		9
<i>Terrestrial group</i>									
Pied Flycatcher	FICUCA	<i>Terr-Trans</i>	<b>4.358</b>	33	47	28	6	5	14
Willow Warbler	PHYLUS	<i>Terr-Trans</i>	<b>3.74</b>	14	18	13	1		6
Common Whitethroat	SYLCOM	<i>Terr-Trans</i>	<b>3.999</b>		1	27	2	8	6
Garden Warbler	SYLBOR	<i>Terr-Trans</i>	2.931	2	3	21	1	4	8
Whinchat	SAXRUB	<i>Terr-Trans</i>	<b>3.7</b>	5	5	10	1		5
Common Nightingale	LUSMEG	<i>Terr-Trans</i>	2.575	4	3	8	6		2
Melodious Warbler	HIPPOL	<i>Terr-Trans</i>	3.172		4	3		5	1
Eurasian Wryneck	JYNTOR	<i>Terr-Short</i>	<b>3.903</b>			4		1	1
Common Redstart	PHOPHO	<i>Terr-Trans</i>	2.385		2	1			
Tree Pipit	ANTTRI	<i>Terr-Trans</i>	2.544	1	1		1		1
Blue tit	PARCAE	<i>Terr-Resid</i>	NA	61	57	41	9	17	25
European Robin	ERIRUB	<i>Terr-Short</i>	2.477	18	41	79	8	16	8
Great Tit	PARMAJ	<i>Terr-Resid</i>	2.436	12	56	12	13	5	2
Blackcap	SYLATR	<i>Terr-Short</i>	2.641		4	35	2	8	8
Chaffinch	FRICOE	<i>Terr-Resid</i>	2.77	7	23		1		1
Common Blackbird	TURMER	<i>Terr-Resid</i>	2.234	4	6	13	6	3	1
Eurasian Wren	TROTRO	<i>Terr-Resid</i>	2.155			15		1	
Song Thrush	TURPHI	<i>Terr-Resid</i>	2.511		2	13	1	2	
Black Redstart	PHOOCH	<i>Terr-Resid</i>	3.395	3	8	1	1		1
European Greenfinch	CARCHL	<i>Terr-Resid</i>	3.221		7	1			
Eurasian Tree Sparrow	PASMON	<i>Terr-Resid</i>	3.338	6					

**Table 6** (continued)

Species	code	Group	SSI	2016			2015		
				MaizeU	MaizeV	Dry-reedbed	MaizeV	Dry-reedbed	Wet-reedbed
<i>Aquatic group</i>									
Common Chiffchaff	<i>Phylloscopus collybita</i>	Terr-Resid	2.892	1	2	3	2	1	
Marsh Tit	<i>Poecile palustris</i>	Terr-Resid	<b>3.72</b>		4		4		
Short-toed Treecreeper	<i>Certhia brachydactyla</i>	Terr-Resid	2.917			3			
Zitting Cisticola	<i>Cisticola juncidis</i>	Terr-Resid	3.078			2			
Lesser Spotted Woodpecker	<i>Dendrocopos minor</i>	Terr-Resid	<b>4.382</b>	1	1				
European Stonechat	<i>Saxicola torquata</i>	Terr-Resid	2.824	2					
House Sparrow	<i>Passer domesticus</i>	Terr-Resid	2.302				1		
Eurasian Sparrowhawk	<i>Accipiter nisus</i>	Terr-Resid	3.006					1	
Red-billed Leiothrix	<i>Leiothrix lutea</i>	Terr-Resid	NA			1			
Hedge Accentor	<i>Prunella modularis</i>	Terr-Resid	2.069			1			1
Firecrest	<i>Regulus ignicapillus</i>	Terr-Resid	3.263		1				

In bold are considered the most specialist species (SSI > 3.5)

Diptera (Bibby and Green 1983; Molina et al. 1998). Those invertebrates were widely available in maize crops, but Cetti's warblers did not use maize crops in our study area. This can be explained by the fact that the adult resident population of this species are territorial in riparian bushlands all year round (Fourcade and Fontanilles 2019; Kennerley and Pearson 2010), while dispersing first-year birds, particularly females, targets reedbeds during this period of the year (Fourcade and Fontanilles 2019).

### Birds' community in maize and reedbed

In this study, we specified which bird species could take advantage of maize crops or reedbeds. Moreover, different habitat use may differ depending on the degree of specialization and the migratory behaviour of the species.

The bird community in maize crops was composed by species that take advantage of the high invertebrate diversity available in the organic maize crops. Bird species occurring in these organic crops are habitat generalists that feed closer to the ground, such as the Bluethroat, Pied Flycatcher and Robin. Pied Flycatchers can feed on arthropods, especially Hymenoptera and Coleoptera on the ground (Cramp 2006; Bibby and Green 1980). In our study, they can even gain more energy in maize crops than in the dry reedbeds. Robins are mainly insectivorous during this period of the year, and like to feed on the ground, ants and beetles, known as main resources or others invertebrates (Tapia 2005; Cramp 2006). The two generalists Blue Tit and Great Tit were more frequently captured in middle and upper height in maize where they can forage upon seeds or arthropods. Blue Tit may actually be very abundant in maize crops (Gottschalk and Cover 2016) and both species may use maize crops to search for food or to transit between woodland habitat patches.

Conversely, aquatic specialists such as migrant *Acrocephalus* and *Locustella* genus were less abundant in crop fields than in reedbed, as Blount et al. (2020) also found. They can find a larger quantity of food resources in reedbeds and selected them over other available wetland habitats (Chernetsov 1998; Chernetsov and Manukyan 1999; Kerbiriou et al. 2010). Furthermore, *Acrocephalus* genus is better adapted to reedbed structure by their capacity to

move on the plant and catch food all along the vertical structure of the habitat (Leisler and Schulze-Hagen 2011). Despite the differences between reedbeds and maize crops in vertical structure (density, diameter, grass layer) and invertebrate availability, *Acrocephalus* can use of the latter habitat to forage. Young Reed warblers get even higher fuel loads in maize crops in our study. They were less numerous in maize, so that they might benefit from lower intraspecific competition. Reed warblers may be also relatively abundant in maize crops (Gottschalk and Cover 2016). Finally, maize crops that is structurally different from reed habitats could provide food, to some categories of aquatic specialists, and may constitute a secondary habitat, although reedbeds, particularly wet ones, would remain the primary selected habitat for migrant aquatic specialists (Berndt and Hölzel 2012).

Another aspect to discuss is the migratory strategy that may influence the use of croplands (Blount et al. 2021). Trans-Saharan insectivorous specialist species need specific habitats as reedbed for efficient refueling to migrate, (Fontanilles et al. 2014; Fourcade et al. 2021). They have long uninterrupted flight bouts between only a few key stopover locations (Pfister et al. 1992; Atkinson et al. 2007). On the other hand, short-distance migrants that use more stopover sites and gather relatively lower fuel loads (Alerstam and Lindström 1990) are likely to utilize a higher diversity of habitats, including farmlands (Blount et al. 2021) and may extend their home range foraging in maize, as Bluethroat do (Fontanilles et al. 2020).

Moreover, the edge habitat effect is positively associated with the birds' use, most likely due to the increased plant diversity (Duckworth 1994; Sapir et al. 2004). Wet or dry ditches, which are all around our fields, may improve the invertebrate diversity and habitat quality. It is the case for Bluethroat around oilseed (Berndt and Hölzel 2012). Another advantage, as in our study site, is to be situated in a major autumn route of migrant. So, crops and reedbeds with nearby bush and grassland in our site can host together a large diversity of migrants as Willow Warbler, Whinchat, Common Nightingale, Garden warbler and Common Whitethroat. Needs of species are also not the same between breeding and post-breeding or migration periods. The migratory birds need to refuel in an area they discover on their arrival and which will not change during the relatively brief stopover. But during the breeding period, the corn is very

small and totally unusable by birds. Breeding species settle territories in other habitats. At the end of the breeding season when the agricultural plot is added to the neighbouring habitats of their territory, they can use maize fields.

Finally, croplands are used by generalists and some migrant or resident species that can forage on a wide range of food types as well as species with preferences for similar habitat in structure to agricultural areas (Blount et al. 2021). In this case, cropland may provide food, but specialist species were less likely to stopover in this habitat.

## Conclusions

The relevance of maize crops differs between bird species depending on their habitat specialization and migratory behaviour. Some anthropogenic habitats, such as organic crops, might contribute to facilitate the migration of some bird species. This could be interesting in a context in which many wetlands cannot be expanded because they are embedded in an urban/anthropogenic matrix, so that organic farming could be an option to improve their stopover. Maize crops may be not a substitution habitat but a supplement one, a human-induced opportunity for migrating and resident birds (Godet et al. 2018; Berndt and Hölzel 2012). Measures to re-naturalise wet habitats or to increase suitability of organic crops for birds around the limited wetland remnants should be encouraged: promote organic farming, avoid insecticide and herbicide or limiting it and create patches without, postponing the harvesting time after mid-October and the end of the insectivorous migration (Dänhardt et al. 2010; Galles et al. 2009). Anyway, this deserves more investigation to be completely and make that positive contribution.

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**Authors contribution** All of the authors contributed to data collection. CK gathered data on bird diet and arthropod availability. PF, IH, and CK analysed the data, designed the methods, and conducted the research. All of the authors took part in the formulation of the questions and hypotheses. PF wrote the paper in cooperation with JMF, IH and CK.

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**Data availability** The data presented in this study are available in this article and from the corresponding author upon reasonable request.

#### Declarations

**Competing interest** The authors declare that they have no conflicts of interest.

**Ethical approval** All data and information from external sources used for the analyses and preparation of the manuscript are properly cited. The conclusions are entirely based on our own results. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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