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Ecologia de parada migratòria de passeriformes al Delta de l'Ebre

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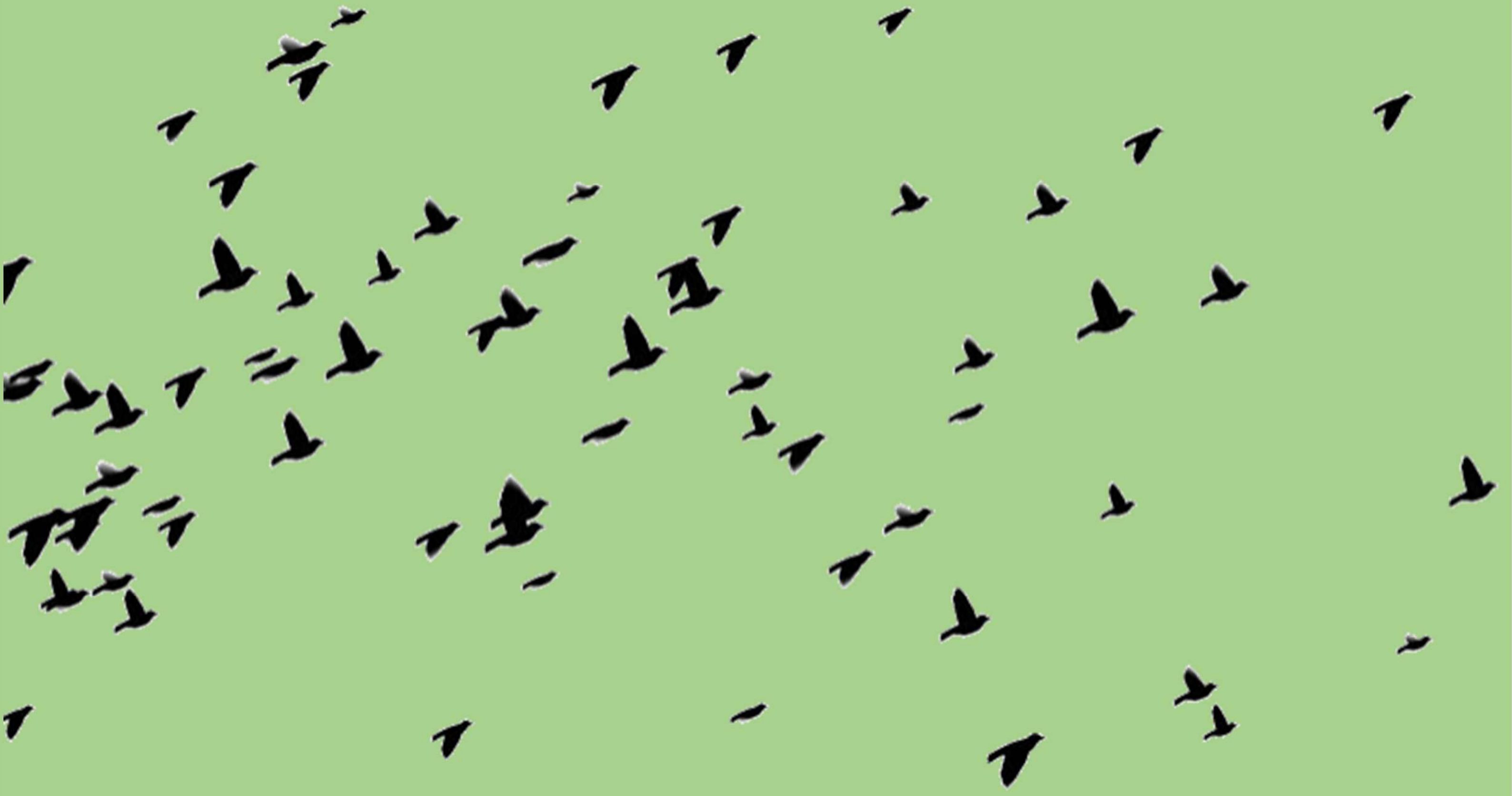

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Departament de Biologia evolutiva, ecologia i ciències ambientals
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Memòria presentada per Ana Sofia Guerreiro Duarte Rivaes da Silva per optar al grau de Doctora per la Universitat de Barcelona

Ana Sofia Guerreiro Duarte Rivaes da Silva

Vistiplau del director de tesi,	Vistiplau del codirector de tesi,
Santiago Mañosa Rifé Departament de Biologia evolutiva, ecologia i ciències ambientals Universitat de Barcelona	**Franz Bairlein** Institute of Avian Research *Vogelwarte Helgoland* Wilhelmshaven, Alemanya

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Una vegada vaig llegir que l'infern és haver d'acabar tots aquells projectes que vas engegar a la vida i que no van tenir un final per culpa de la falta de temps o perquè hi vas perdre l'interès. Aquesta tesi estava a punt de convertir-se en un projecte d'aquest tipus però aquí està la prova de que mai és tard per res.

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Seguim juntes en aquest projecte de futur i no cal patir perquè tinc fama de fer-ho tot molt llarg...

We have no past, we won’t reach back
Keep with me forward all through the night
And once we start, the meter clicks
And it goes running all through the night.
Until it ends, there is no end.
“All through the night”, Cyndi Lauper (Jules Shear)

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CHAPTER I

General Introduction

Migration associated with movements between breeding and wintering areas allow animals to maximize fitness in response to seasonal changes in resources (Dingle 2014). Some of the most incredible migrations in the animal world are performed by birds which are possibly one of the best-studied migratory groups. Almost 20% of avian species are migratory (Kirby *et al*. 2008). Birds are well adapted for migration because first, they can fly, second, they display efficient behaviour and third, they show an extraordinary physiological and morphological adaptability (Newton 2008). Although flapping flight is one of the most energetically costly forms of locomotion, greater than either running or swimming, the high speeds of migration achieved makes flight an overall more energy efficient form of transport (Butler 1991). To perform long migration flights, birds use mainly fat as fuel source, and it contributes with about 95% of the energy required (Jenni and Jenni-Eiermann 1998). The rest is derived from lean mass catabolism (Klaassen and Kvist 2000; Guglielmo *et al*. 2017). Prior to migration, birds accumulate fat stores that may account for up to 50% of their body mass (Nielsen and Riis 2013) and once these fat stores are depleted after a flight bout they are replenished at stopover sites along the migration route. Some of these stopover sites may be high quality feeding grounds where birds can refuel quickly to continue their migratory journey, or just resting spots where birds can avoid flying in hazardous weather or stop after a long flight.

Migration is a dangerous life stage, which means that migrants have higher probability of perish while migrating than non-migrants. The mortality rates during the migratory period may be at least 15 times higher compared to that in the stationary periods of the annual life cycle (Sillett and Holmes 2002). Moreover, imagine small passerine birds, many of them inexperienced birds, born only some months before the beginning of migration, sometimes weighting just 10g or less, flying by night thousands of kilometres to encounter new kinds of habitats (Mettke-Hofmann and Greenberg 2005), competition for food resources (Moore and Yong 1991), predators (Lindström 1989), and inclement weather (Newton 2007), all while needing to maintain adequate fat reserves to perform their long-distance flight successfully. In fact, migrant bird populations suffer nowadays a sustained decline as shown in analyses of bird population trends across Europe (Sanderson *et al*., 2006; Vickery *et al*. 2014), North America (Ballard *et al*. 2003) and East Asia (MacKinnon *et al*. 2012). This decline is strongly associated with the accumulative impact of certain human activities such as habitat loss (Aharon-Rotman 2016), hunting (Raine 2016, Clausen *et al*. 2017) and climate change (Jiao *et al*. 2016) on the areas used by birds in their migratory routes (Crick 2004), especially on stopover sites (Bairlein 2016). For instance, coastal development and urban expansion continuously invades wildlife habitats which have the potential to be important stopover sites for migrating songbirds (Bonter *et al*. 2009). Therefore, the knowledge of the relationships between migratory species and these migration hot spots must be the basis of any conservation strategy aimed at protecting these species. Understanding the quality and availability of highly used stopover sites is vital for migratory bird conservation (Mehlman *et al*. 2005) and to know where migratory birds stop during their migrations and how the sites function for migrants will provide information for conservation and management of suitable stopover areas and therefore, help in the development of full-life-cycle specific conservation plans.

The Iberian Peninsula geographically connects Africa and Western Europe and migrants use it in transit between breeding and wintering grounds during both migration periods (Newton 2008). It becomes an ideal scenario for the study of migratory strategies (Bruderer and Liechti 1999) especially if we consider also Mediterranean wintering birds. In the case of the trans-Saharan species, during their post-breeding migrations, the Iberian Peninsula is one of the last opportunities to stock up on the necessary reserves to cross the Mediterranean Sea and the Sahara Desert, being a key area for the success of their journey (Moreau 1956). Most of the time that birds spend migrating they are not flying but sedimented in stopover areas either to rest or to replenish fat reserves (Hedenström and Alerstam 1997). As migrants use to follow the coast until they reach the bottleneck point where crossing the Mediterranean ecological barrier is easier, many stopover areas are coastal wetlands, habitats with high conservation interest since they give refuge to great biological diversity. Wetlands play therefore, a key role at a decisive moment in the life cycle of many migrant species (Tucker and Evans 1997).

This thesis focusses on the significance of the Ebro delta, as the second most important wetland in the Western Mediterranean, for the migration of songbirds and draw an overall picture of the way migrant passerines use the area as a stopover site. Since the Ebro delta is a highly humanized area where several important economic activities take place (e.g. rice production, hunting, fishing and tourism), as well as a very fragile territory due to severe problems of coastal regression and subsidence, the information here gathered aims to help in future conservation plans that should take into account not only breeding species but also wintering and migrating ones, what will give even more importance to this coastal wetland, which we must protect at all costs.

Therefore, this thesis work overs the behaviour of both short/medium and long-distance migrants, i.e. Mediterranean wintering and trans-Saharan species, during their stopover at a coastal lagoon in the Ebro delta during both migration seasons (spring and autumn). It starts with the questions of when and how do songbirds use the stopover site and continues with how long they use it and the extrinsic and intrinsic factors influencing their stopover decisions (migration behaviour, age classes, body condition and endogenous time programme). Once we know the phenology patterns and stopover durations as well as body condition of birds at arrival, the next step is to investigate which type of stopover area we are dealing with. That is, if birds increase fat stores and have long stopovers (and we are facing a refuelling area) or birds stay only for a rest between flight bouts maintaining their actual fat stores to resume migration as fast as possible. If we are facing a resting site, the best way to approach energetic problems is visualizing what happens in a day of the life of these migrants. That means also that transients will probably opt to leave the area the same day of arrival. Finally, we describe habitat preferences of these migrant species particularly the differences between habitats where the reed is dominant with other habitats where bushes are more important, as if the vegetation type could be key to defining the suitability of a determined stopover site (Ktitorov *et al.* 2008). The main conductive thread of this thesis is then body condition of birds during stopover and how it is affected by, or affects, different migration strategies during both migration periods. This story line conducts to the most reliable picture of songbird migration in the Ebro delta.

The tool used to investigate the issues exposed above was a cheap one and available to everyone who asks for it: the ring-recovery data. Bird ringing is long used to study migration processes, and although nowadays more trendy and modern methods are available (e.g. satellite telemetry, geolocation loggers), not all of them are affordable to everyone who wants to use them. If we realize that the EURING Data Bank (EDB) is a unique set of mark–reencounter data on European birds with more than 10 million encounter records and that is at the disposal of the scientific and conservation communities (du Feu *et al*. 2016) and that ringing is still required as the key technique for facilitating our understanding of migration (Bairlein and Schaub 2009), we can use its potential to evaluate the importance of stopover areas and contribute to their conservation and also of the species that depend on these areas to survive. Of course, the new methods are very useful and sometimes a lot more precise and the combination of these methods with ringing data will improve considerably our knowledge about the migration phenomenon in the future. But while we look for financing to tag our birds with geolocators, let's start working out the more basic questions.

Aims

The main aim of this thesis is to explore the stopover ecology of songbirds with different migratory behaviour (trans-Saharan and Mediterranean wintering species) during pre-breeding and post-breeding migration seasons in the Ebro delta (NE Spain) using data from standardized bird-ringing campaigns. I investigate the factors influencing seasonal occurrence, body mass, stopover duration, fuel deposition and habitat preferences of six target species at a stopover site, analyse its quality as a refuelling site and propose some conservation measures for other coastal wetland type stopover areas that are not facing an ecological barrier.

The specific goals of the thesis are:

1- To investigate de phenology of passage and specific body condition of migrants at arrival and its variation with the progress of season.
2- To evaluate how extrinsic and intrinsic factors influence the time and energy components of stopover and define the migration behaviour of the study species.
3- To estimate diurnal body mass changes and the possible factors that could affect this variation, focusing on transients, i.e. birds that stopover only for one or two days, and compare diurnal fuel deposition rates with daily rates estimated previously.
4- To investigate the possible factors affecting habitat preferences of transients during stopover and its relation to body condition.

Thesis outlines

The thesis is developed in seven chapters. The first two are destined, one to a general introduction (Chapter 1) with some general background about the main theme of the thesis and the line of reason to be discussed, main objectives and thesis outlines, and the other to the description of the study area and study species (Chapter 2). More concrete methodology and statistical analyses description is included in the following four chapters, that form the core of the thesis research (Chapter 3 to 6). These chapters follow a line of argument that cover as much as possible the behaviour and ecology of migrants during stopover in the Ebro delta in both migration seasons, with the final goal of assessing the suitability of the area as a stopover site. A general discussion follows (Chapter 7) that links and addresses several of the issues examined in each previous core chapters and ends with the main conclusions enumerated.

The core research chapters are briefly summarized in the following lines:

Chapter 3. Don’t pass me by: when and how migrants arrive in the Ebro delta?

This chapter is the starting point to the study of stopover ecology of migrant songbirds in the Ebro Delta. First, we study the timing of passage, that is, when are birds present at the stopover site through the analysis of the phenology of six passerine species with contrasting general migratory behaviour, during both spring and autumn migration periods. Second, to understand why and how migrants use the area, we analyse specific body condition (body mass and fat stores) at arrival and how it varies with the progress of season. We then analyse possible differences in phenology and body condition between long and short-distance migrants and age classes, within-season variation and at the end we compare both post and pre-breeding migration seasons.

Chapter 4. Should I stay, or should I go: extrinsic and intrinsic factors influencing stopover decisions of songbirds with different migration strategies in the Ebro Delta.

Once we know when and how migration occurs at our site, in this chapter we investigate how much time birds spend in stopover and how birds manage the energy necessary to complete migration successfully. We analyse stopover length and fuel deposition rates, during both migration periods, among species with different migration behaviour, as well as specific differences between age classes related to both migration components. We will focus also on the body condition of birds at arrival and their endogenous time programme. Finally, to wrap the research we consider our results in relation to actual optimal migration strategy theories and discuss the significance of the Ebro delta as a suitable stopover area for songbirds with different migration strategies.

Chapter 5. Tonight we fly: a day in the life of transient songbirds regarding body mass variation.

With the first questions (when, for how long and how) sorted out, we go deep on diurnal behaviour of migrants, specially transients as they are majority at our stopover site. We first reveal diurnal activity, then estimate diurnal body mass changes of transients and finally analyse age differences, body condition at arrival, species with different migration behaviour and birds at different migration stages. During the analyses we compare diurnal and daily fuel deposition rates (obtained in Chapter 4). We finish the chapter detecting possible variations in weight around dusk, when birds start their period of restlessness and prepare for a new nocturnal flight, as a predictor of their departure intentions. The final goal of the chapter is to identify suitable one-day stopover areas for transients.

Chapter 6. This must be the place: habitat preferences of migrant songbirds during stopover in a coastal location.

In this chapter we solve the last question of this thesis thread: where? We approach habitat preferences of migrants, especially transient birds and compare specific body condition in two different habitats (reedbed and bushes). We use migration season, species migratory status as short/medium- or long-distance migrants, species and body condition at arrival as factors to model habitat preference and identify suitable stopover sites along the migratory route.

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CHAPTER II

General Methods

Geographical context: the Ebro delta

The Ebro delta (NE Iberian Peninsula) with an area of about 320 km^2, is the second largest coastal wetland in the Western Mediterranean, and one of the most important in Europe (Figure 2.1). From an ecological point of view, the Ebro delta stands out by a rich diversity of habitats in a considerably small area and consequently very high biodiversity levels. This area excels fundamentally by its ornithological and ichthyological fauna, as well as by its flora from halophile environments. A significant amount of these habitats and species are very scarce in the Mediterranean and European context, so that their conservation is of utmost priority to maintain their biodiversity.

This biological richness contrasts with a deep human presence. Natural habitats cover about the 25% of the total delta surface and more than 20.000 ha of the delta plain are occupied by rice fields. In order to make possible the harmony between natural values and their human exploitation, almost 8.000 ha of the delta, mostly coastal areas (coastal lagoons, sand spits and brackish marshes), are declared protected as Natura 2000 site of the European Union, as Natural Park and also Biosphere Reserve (UNESCO).

Study site: The Canal Vell Lagoon

The ringing campaigns were carried out at the Canal Vell Biological Station (UTM 31T 4512629 N; 313110 E) in the Ebro Delta Natural Park at the northern shore of the Canal Vell lagoon (Figure 2.1). Reedbeds, the dominant vegetation of the study site, are composed mainly by *Phragmites australis*, *Typha* sp. and *Scirpus maritimus*, mixed with open water areas. Other habitat types, like some patches of *Tamarix sp.* and a line of *Myoporum tenuifolium*, planted in the early 90s, are also present. The surrounding areas of the lagoon are composed mainly of rice fields.

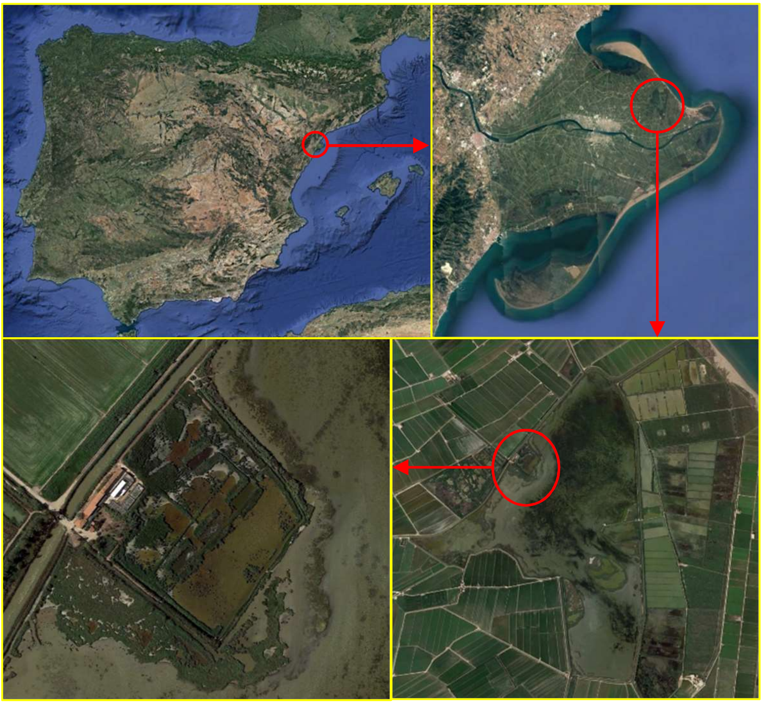

Figure 2.1. Map of the location of the study site, the Canal Vell Biological Station in the context of the Canal Vell coastal lagoon, the Ebro delta and the Iberian Peninsula.

Study species

This thesis is focused on a few of the most common passerine species often seen in the Ebro delta during both autumn and spring migration periods. The different species were selected because they were regularly caught in the standardized ringing programme at Canal Vell Biological Station and because they have different migratory strategies. Most of the species are well studied within the Palaearctic-African migratory flyway, which facilitates comparisons to other studies.

We have studied three trans-Saharan long-distance migrants, Reed warblers *Acrocephalus scirpaceus* (Figure 2.2), Willow warblers *Phylloscopus trochilus* (Figure 2.3) and Pied flycachers *Ficedula hypoleuca* (Figure 2.4). These species breed throughout the Western Palaearctic and spend the winter in tropical Africa south of the Sahel region (del Hoyo *et al*. 2006). Some hundreds of pairs of Reed warblers also breed in the Ebro delta (Fouces 2004).

On migration Reed warblers (8 – 19.7g) occur in reeds, thickets and tall grass. They feed mainly on insects and their larvae, but seeds and unidentified plant material were also found in stomachs content analyses. The species is considered opportunistic and is able to take advantage of local short-lived sources of abundant food (chironomid flies, aphids, mosquitoes). Swarms of flying ants may constitute important food during migration and in winter quarters. They caught their prey mainly from reed stems and blades, bushes and occasionally from ground (del Hoyo *et al*. 2006).

Figure 2.2. Reed warbler (*Acrocephalus scirpaceus*)

Willow warblers, a relatively small bird (6.3 – 14.6g), occur on passage almost anywhere where trees, bushes or coastal scrub are present. Feed mostly on insects and their eggs and larvae but also on some plant material. They chiefly take insects from among foliage, but also at lower levels in trees, bushes and low vegetation, and on the ground during cold or wet weather conditions (del Hoyo *et al*. 2006).

Figure 2.3. Willow warbler (*Phylloscopus trochilus*)

Pied flycatchers (9.7 – 22.2g) during migration often use dry and bushy areas while feeding mostly on insects, both flying and non-flying ones, but can take also spiders and other invertebrates and occasionally take fruits and seeds. Foraging behaviour includes all levels in shady to more open trees, and in tall bushes, searching and gleaning from foliage and branches (del Hoyo *et al*. 2006).

Figure 2.4. Pied flycathcer (*Ficedula hypoleuca*)

To enable comparisons with long-distance migrants, we also studied three Mediterranean wintering short to medium-distance migrants, Bluethroats *Luscinia svecica* (Figure 2.5), Cetti's warblers *Cettia cetti* (Figure 2.6) and Chiffchaffs *Phylloscopus collybita* (Figure 2.7). These species occur throughout most of the Western Palaearctic, migrating shorter distances to winter in the Mediterranean region (del Hoyo *et al*. 2005, 2006). All three species have wintering populations in the Ebro delta (Barriocanal and Aymí 2011, Copete and López 2011, Rivaes 2011) and Cetti's warblers are also present during the breeding season (Rivaes and Riera 2004).

Bluethroats, that weight between 12 and 25g, are present in winter, among other habitats, in vegetation close to both fresh and salt water, in reedbeds, withered saltmarsh vegetation and tamarisk scrubs, all present at our site. They feed on invertebrates, insects and during migration also on seeds and fruits. Feeding movements during winter consist on hopping about water's hedge, skulking among wet reeds and bushes (del Hoyo *et al*. 2005).

Figure 2.5. Bluethroat (*Luscinia svecica*)

Cetti's warblers (8 – 18.5g), in non-breeding areas may occur in variably wet or dry scrub, tamarisk (*Tamarix* sp.) scrub and other dense cover near water, marshes, swamps and reeds. They feed mostly on macroinvertebrates and occasionally on small seeds, taken from ground, within vegetation or from surface of water and on occasions pursues insects in flight (del Hoyo *et al*. 2006).

Figure 2.6. Cetti's warbler (*Cettia cetti*)

Chiffchaffs, the smallest of the short-distance species chosen (6 – 10.9g), during non-breeding season inhabits a variety of woodland habitats, from small clumps of coastal scrub to willow thickets and reedbeds, feed mostly on insects and small molluscs. During autumn, they also take seeds and berries. Forages at all levels by taking insects from among foliage in trees, bushes and low vegetation, sometimes from the ground.

Also hovers and make short dashing sallies or picks prey from surface of water (del Hoyo *et al*. 2006).

Figure 2.7. Chiffchaff (*Phylloscopus collybita*)

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CHAPTER III

Don't pass me by: when and how migrant songbirds arrive in the Ebro delta?

INTRODUCTION

Twice a year more than two billion songbirds undertake long distance flights of thousands of kilometres between their breeding grounds in Europe and their winter grounds somewhere from the Mediterranean region to sub-Saharan Africa (Moreau 1972, Hahn *et al.* 2009). Their migratory journeys are carried out in multiple ways (Alerstam 2011) but to optimize the entire process of migration, which includes flying and stopover, migrants may be selected primarily to: (1) minimise the time spent on migration (to migrate as fast as possible), (2) minimise energy expenditure (keeping the flight costs low by storing only as much fat as is needed to reach the next fat deposition site) or (3) minimise overall predation risks, if there is a significant predation pressure during migration (Lindström and Alerstam 1992). In this context, coastal areas of the Mediterranean region may provide important stopover sites where birds can refuel or recover for further migration (Schaub and Jenni 2001, Maggini and Bairlein 2011, Arizaga *et al.* 2013). Stopover is then the most flexible and thus decision-prone main phase of migration and birds' behaviour during this stage may reveal specific migration strategies (Schmaljohann and Booth 2017).

The first approach to know the stopover ecology of songbirds during migration is then the study of their phenology passage, that is, when are birds present at the stopover site. In this chapter we will analyse the phenology of six passerine species with contrasting general migratory behaviour, which stopover in the Ebro Delta during both spring and autumn migration periods: three long-distance migrants that cross the Sahara (Reed warblers *Acrocephalus scirpaceus*, Willow warblers *Phylloscopus trochilus* and Pied flycachers *Ficedula hypoleuca*,) and three short/middle-distance migrants, that winter in the Mediterranean basin (Cetti's warbler *Cettia cetti*, Bluethroat *Luscinia svecica* and Chiffchaff *Phylloscopus collybita*).

Once you know when birds use the stopover site the next step is to understand why and how they use it. Therefore, we analyse specific body condition (body mass and fat stores) at arrival and how it varies with the progress of season. Moreover, as migration behaviour may vary amongst species with different migration strategies and within species, we analyse possible differences in phenology and body condition between long and short-distance migrants and between ages. We also investigate within-season variation, as timing of migration may influence stopover decisions and fuelling, and finally we compare both post and pre-breeding migration seasons. Understanding stopover behaviour during both migration seasons is crucial to recognize the entire migration strategy of migrating birds (Weber *et al.* 1999). To establish a picture of the stopover dynamics of several songbird species at our area will provide conservation management tools to insure suitable habitats for migrating birds.

STUDY AREA AND METHODS

The study was carried out at the Canal Vell lagoon, in the Ebro Delta, NE Spain (UTM 31T 4512629 N; 313110 E). This coastal lagoon is surrounded by large extensions of flooded reedbed (*Phragmites australis, Typha angustifolia*) and some shrub areas (*Myoporum tenuifolium* and *Tamarix sp.*) (see Chapter 2 for a detailed description of study site). Birds were captured during both autumn (1992-2000) and spring (1996-2000) migration and were ringed and aged according to Svensson (1992) and Jenni and Winkler (1994). Body mass (to the nearest 0.1g) was recorded using an electronic scale. Wing length was measured to the 0.5mm using method 3 of Svensson (1992). Fat classes were scored from 0 to 8 following Kaiser (1993). Dates were grouped in standard 5-day periods (pentades) according to Berthold (1973), where pentade 1 refers to the first five days of the year and pentade 73 the last five days of the same year.

Statistical analysis

All years were pooled for general phenology analysis, although differences in year by year median date of passage existed for autumn migration. However, standard deviation of the mean median pentade was less than 1,5 pentades for half of the species (Table 3.1). For spring migration median date of passage was similar between years.

Table 3.1. Annual passage median pentades, sample size (in brackets), mean median passage (mean±SD) and level of significance of the Kruskall-Wallis independent samples median test amongst years for all studied species during autumn.

Year	Cetti's warbler	Bluethroat	Chiffchaff	Reed warbler	Willow warbler	Pied flycatcher
1992	54 (614)	54 (151)	59 (68)	50 (1331)	50 (78)	52 (55)
1993	55 (1190)	53 (85)	64 (1537)	50 (1516)	50 (53)	54 (22)
1994	55 (899)	55 (93)	63 (1485)	51 (1639)	52 (76)	53 (64)
1995	55 (1468)	57 (118)	64 (1537)	49 (1519)	50 (116)	52 (57)
1996	56 (948)	55 (103)	63 (689)	50 (1244)	50 (78)	52 (63)
1997	54 (1241)	56 (97)	64 (988)	51 (1437)	51 (111)	52 (38)
1998	55 (1070)	53 (89)	63 (1189)	52 (1355)	53 (57)	53 (51)
1999	56 (575)	56 (107)	63 (709)	51 (1641)	51 (74)	51 (110)
2000	56 (803)	54 (137)	64 (1251)	51 (1387)	51 (107)	52 (187)
Mean ± SD	55.11±0.78	54.78±1.39	63.00±1.58	50.56±0.88	50.89±1.05	52.33±0.87
K-W	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**

Interspecific differences in capture frequency distribution were tested using the Kruskal-Wallis for independent samples test and the Kolmogorov-Smirnov test to compare the phenology patterns between birds of different migration status (Mediterranean wintering vs trans-Saharans). Specific age differences analyses were performed only for post-breeding migration and were tested for phenology patterns using the median test (Sokal and Rolph 1995). We also investigated possible within-season variation in body mass and fat score, for autumn migration with a General Linear Mixed Model (GLMM) and for spring data with a General Linear Model of covariance analysis (ANCOVA) instead, because there was no year to year variation in the distribution of the data. We used body mass and fat score as dependent variables, time (measured in pentades) as covariate and age as grouping variable (only in autumn). Wing length was introduced as a covariant for body mass analysis, in order to correct for body size variation, and year as random factor to correct for year to year variation (in autumn). We also modelled wing vs. time interaction for body mass analysis and age vs. time interactions for both dependent variables, body mass and fat scores. We used Type I sum of squares where the effect of a variable is evaluated only after adjustment for the ones entered previously.

Moreover, we split autumn migration in three periods and defined them as: early (≤10% of total captures), main (±80% of total captures) and late migrants (≤10% of total captures) and used the one-way analysis of variance (ANOVA) to compare standard body mass (the ratio of weight by wing length) and fat score of birds captured at the three different migration periods as well as for interspecific comparisons, followed by a post-hoc test for multiple comparisons.

Finally, to compare specific values of body characters between spring and fall migration we used the t-test for independent samples, preceded by the Levene's test for equality of variances. All statistical tests were performed with SPSS 24.0 package (SPSS Inc. 2016).

RESULTS

Phenology patterns

In autumn, species differed in their timing and pattern of captures (Kruskal-Wallis test, $\chi_{(5)}$=21552.9, *p*=0.000) (Figure 3.1). Reed warblers started their passage already in August followed by Willow warblers and Pied flycatchers which had their peak of passage during the first half of September. Bluethroats and Cetti's warblers' passage occurred in September-October and Chiffchaffs migrated later, mostly in November with figures skewed towards the end of season. Trans-Saharan migrants tended to migrate earlier than Mediterranean wintering species (Kolmogorov-Smirnov test, D=53.641, *p*=0.000).

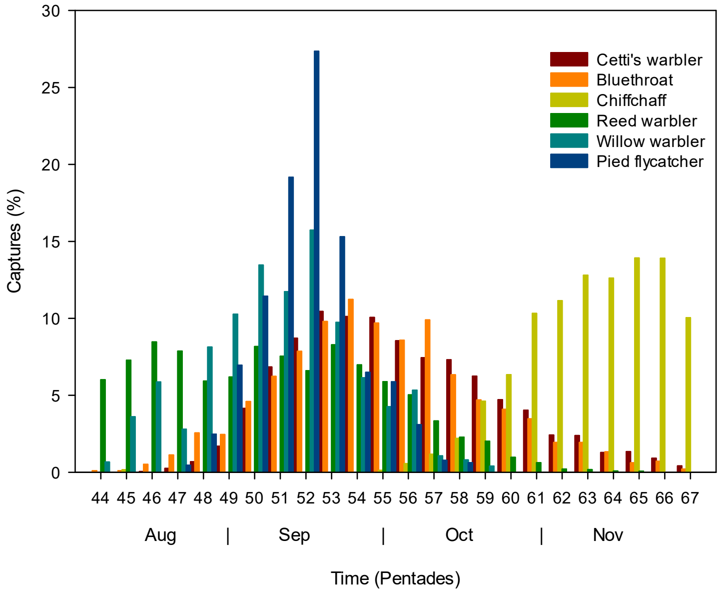

Figure 3.1. Seasonal distribution of autumn captures for the six studied species, three Mediterranean wintering and three trans-Saharan.

First-year Cetti's warblers and Chiffchaffs occurred at our site significantly earlier than adults, while adult Reed warblers left the area before first-year birds (Table 3.2), showing significant differential migration with age.

Table 3.2. Capture totals, median dates of passage (median pentade in brackets) and median test statistic for age differences in autumn phenology.

	Captures			Median date (pentade)			Median Test	
Species	Total [a]	Adults	1-year	Total	Adults	1-year	Chi-square	P-value
Bluethroat	980	268	706	29 Sep (55)	28 Sep (55)	29 Sep (55)	0.93	0.335
Cetti's warbler	8808	454	7448	1 Oct (55)	6 Oct (56)	1 Oct (55)	15.92	**0.000**
Chiffchaff	9453	2085	5531	12 Nov (64)	15 Nov (64)	11 Nov (63)	32.03	**0.000**
Reed warbler	13069	2551	10476	8 Sep (51)	16 Aug (46)	14 Sep (52)	1871.92	**0.000**
Willow warbler	750	54	607	9 Sep (51)	8 Sep (51)	10 Sep (51)	0.13	0.718
Pied flycatcher	647	78	566	15 Sep (52)	15/16 Sep (52)	15 Sep (52)	2.35	0.125

[a] Total captures number includes birds of unknown age.

For spring migration analysis, Bluethroats and Cetti's warblers were excluded due to very low capture rates (2 and 8 captures, respectively). Moreover, due to the short ringing campaigns (one month), the phenologies of passage of most of the other studied species were less defined, nevertheless they show different distributions (Kruskal-Wallis test, $\chi_{(5)}$=21552.9, p=0.000). All three trans-Saharan species were caught throughout the entire period with Willow warblers passing earlier than Pied flycatchers and Reed warblers, respectively. Chiffchaffs were captured mainly in the first pentade of the trapping period, and although passage is truncated, it seems they migrate earlier than the long-distance migrants (Kolmogorov-Smirnov test, D=2.975, p=0.000) (Figure 3.2).

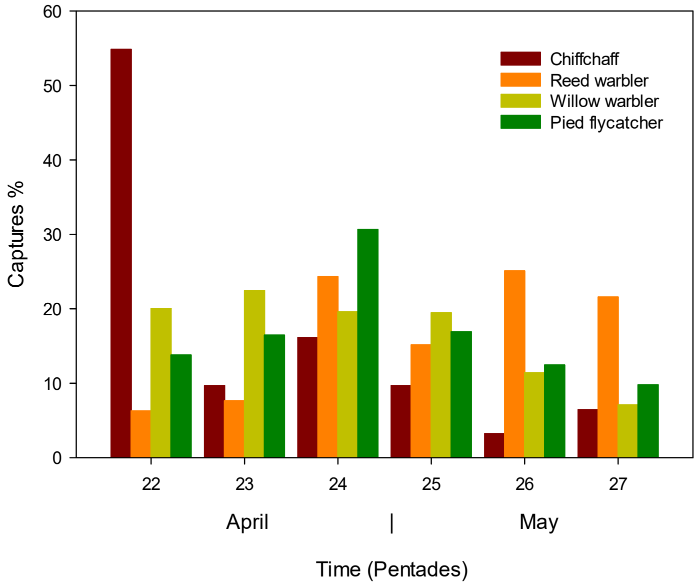

Figure 3.2. Seasonal distribution of spring captures for four of the studied species, three trans-Saharan species and one Mediterranean wintering.

Body condition

During autumn, adult Mediterranean wintering birds were significantly heavier than first-year birds caught at the same time (Table 3.3), but only Bluethroats and Chiffchafs were significantly fatter. For Cetti's warblers differences in weight reflect size differences between both ages but not different fat accumulation index. Regarding trans-Saharan migrants only Reed warblers showed age differences for body mass and fatscore. Adults were heavier than first-year birds, but they carried less fat instead.

Table 3.3. Adult and first-year mean body mass and fat score at first capture during autumn migration.

	Body mass						Fat score					
	Adults		1-year		ANOVA		Adults		1-year		ANOVA	
Species	N [a]	Mean ± SE	N [a]	Mean ± SE	F	P	N [a]	Mean ± SE	N [a]	Mean ± SE	F	P
Bluethroat	266	16.22 ± 0.09	693	15.92 ± 0.05	9.13	**0.003**	267	2.20 ± 0.07	704	1.90 ± 0.04	14.39	**0.000**
Cetti's Warbler	446	11.24 ± 0.05	7351	11.07 ± 0.01	8.98	**0.003**	451	1.99 ± 0.04	7403	1.93 ± 0.01	1.90	0.168
Chiffchaff	2049	7.58 ± 0.01	5437	7.30 ± 0.01	250.69	**0.000**	2057	2.51 ± 0.02	5465	2.24 ± 0.01	107.77	**0.000**
Reed Warbler	2511	11.60 ± 0.03	10314	11.42 ± 0.02	29.23	**0.000**	2496	2.87 ± 0.03	10413	2.99 ± 0.01	13.81	**0.000**
Willow Warbler	52	9.09 ± 0.21	601	9.03 ± 0.06	0.07	0.788	53	3.35 ± 0.17	606	3.26 ± 0.05	0.24	0.624
Pied Flycatcher	76	15.00 ± 0.20	561	14.55 ± 0.09	3.13	0.077	78	3.79 ± 0.11	566	3.54 ± 0.05	2.88	0.090

[a] Total number of birds with valid body mass and fat score values. This number is different from total number of birds captured.

For most of the species from both migration status weight and fat stores increased with time, and late birds were heavier and fatter than early migrants. Only Chiffchaffs and

Cetti's warblers showed a negative tendency of fat scores over time that was contrary to the body mass variation (Figures 3.3 and 3.4).

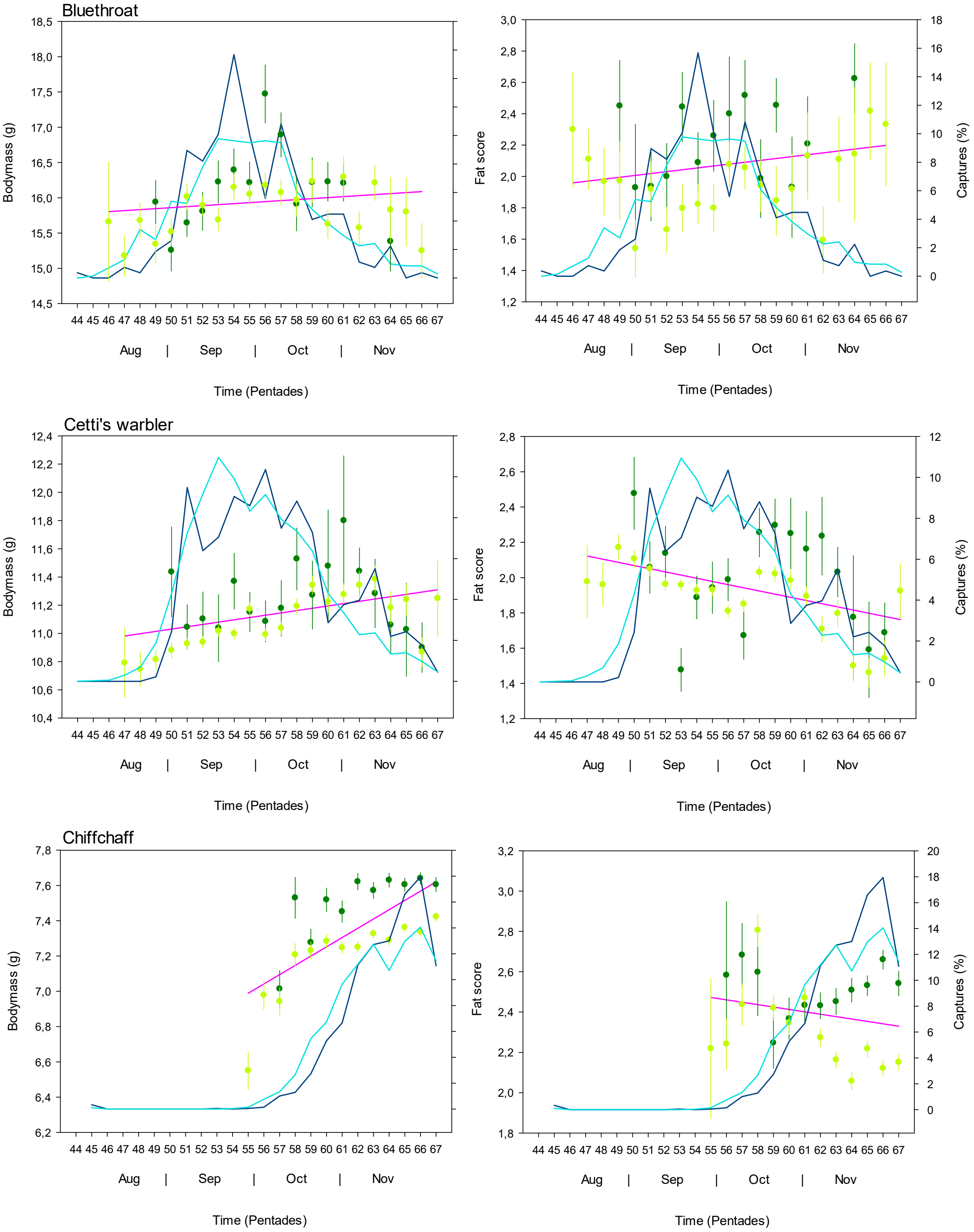

Figure 3.3. Seasonal distribution (line plots; both columns), mean body mass ± SE (dots, left column) and fat score ± SE (dots, right column) variation for adult (dark colour) and first-year (light colour) Mediterranean wintering birds during autumn migration at Canal Vell. In pink, regression line for all data on plot of the dependent variable (body mass or fat score) with time.

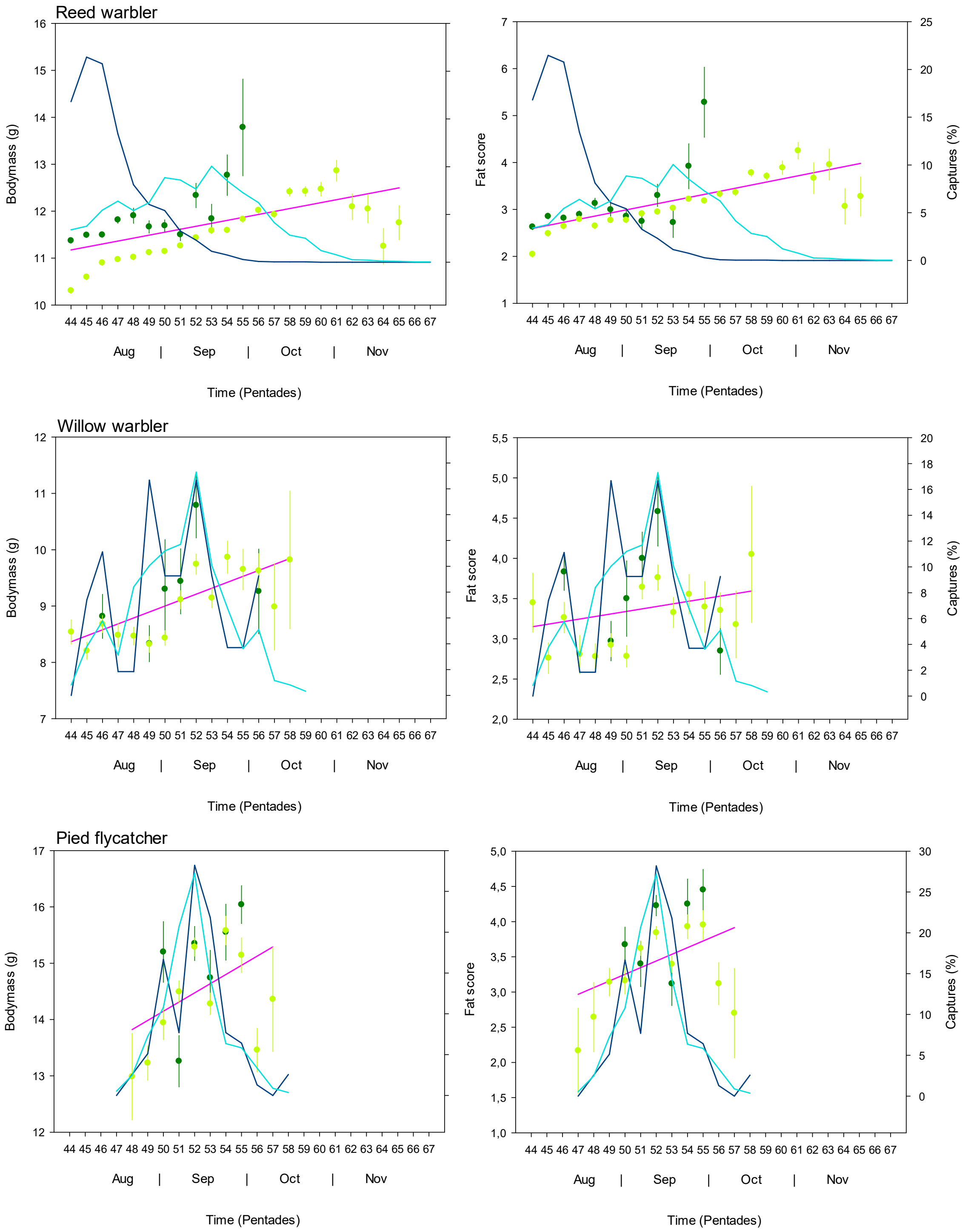

Figure 3.4. Seasonal distribution (line plots; both columns), mean body mass ± SE (dots, left column) and fat score ± SE (dots, right column) variation for adult (dark colour) and first-year (light colour) trans-Saharan birds during autumn migration at Canal Vell. In pink, regression line for all data on plot of the dependent variable (body mass or fat score) with time.

The GLMM analysis reveals that correlation of body mass with wing occurred for all species during autumn migration due to the expected relation between size of birds and its weight and at least for Cetti's and Willow warblers the interaction of wing with time of capture affected also body mass (Table 3.4). Body mass varied additionally with time of capture for all species but Bluethroats.

Although some species showed age differences in their phenology, as we have seen before, age contributed to the variation of body mass, after taking in account size and time, only for Reed and Cetti's warblers. Moreover, for Cetti's warblers and Chiffchaffs the relationship between body mass and age depended also from time of capture (Table 3.3). Finally, the most pronounced autumnal body mass increases were found for Chiffchaffs and Pied flycatchers (Figure 3.3 and 3.4).

Table 3.4. GLMM significance levels for body mass in response to the random factor year, the fixed factor age and the covariates wing and time, during autumn migration. The test is adjusted (Type I error).

			Body mass P-values[a]			
Factor/Variable	Bluethroat	Cetti's warbler	Chiffchaff	Reed warbler	Willow warbler	Pied flycatcher
Year	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Wing	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Time	0.117	**0.000**	0.225	**0.000**	**0.000**	**0.000**
Wing*Time	0.669	**0.000**	0.964	0.189	**0.008**	0.436
Age	0.226	**0.000**	0.245	**0.000**	0.558	0.286
Age*Time	0.657	**0.015**	**0.024**	0.542	0.975	0.526
N adults	176	265	1708	1673	38	51
N 1st-year	455	5532	3679	6690	471	448

[a] P-value = level of significance

Mean weight was significantly different between the three main periods of migration (early, middle and late migration) within all species, with early migrants being significantly lighter than middle and late migrants. Both late trans-Saharan and Mediterranean wintering migrants were significantly heavier in almost all species. Only Bluethroats and Pied flycatchers were heavier during the main migration period (Table 3.5 – Figure 3.5).

Table 3.5. Mean body mass comparison between early, main and late migrants during autumn migration.

Species	Early		Main		Late		ANOVA
	N	Mean± SE	N	Mean± SE	N	Mean± SE	P [a]
Bluethroat	66	15.50 ± 0.14	834	16.07 ± 0.05	65	15.79 ± 0.12	**0.002**
Cetti's Warbler	597	10.82 ± 0.04	7329	11.08 ± 0.01	761	11.25 ± 0.04	**0.000**
Chiffchaff	838	7.18 ± 0.03	7541	7.38 ± 0.01	922	7.49 ± 0.02	**0.000**
Reed Warbler	760	10.90 ± 0.04	10848	11.40 ± 0.01	1254	12.24 ± 0.04	**0.000**
Willow Warbler	74	8.55 ± 0.10	611	9.02 ± 0.06	57	9.42 ± 0.24	**0.000**
Pied Flycatcher	64	13.26 ± 0.27	547	14.80 ± 0.09	28	13.70 ± 0.32	**0.000**

[a] level of significance

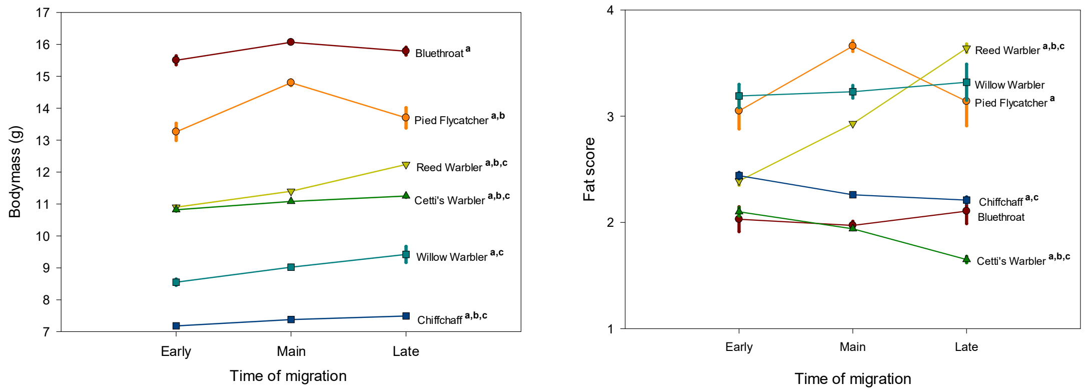

Figure 3.5. Mean (± SE) body mass and fat scores of each species at different stages of migration (early, main and late migrants). a, b and c mean significant differences in values between early - main, main - late and early - late migrants, respectively.

After correcting for year variation, fat stores were correlated with time of capture in autumn for both trans-Saharan and Mediterranean wintering species, except for Bluethroats (Table 3.6). Age influenced the response of fat scores for Mediterranean wintering species, as well as for Reed warblers. For Cetti's warblers, Chiffchaffs and Willow warblers Time interacted with age affecting body mass.

Average fat scores were species specific and during autumn Pied flycatchers carried more fat than all the other species, followed by Willow and Reed warblers, respectively. The three tropical migrants were fatter than the short-distance ones (Table 3.7). Bluethroats and Cetti's warblers showed similar average fat scores (Tanhane test: *p*=0.867).

Fat scores varied significantly between migration blocks except for Bluethroats and Willow warblers (Table 3.8). Reed warblers' fat scores increased significantly while

Chiffchaffs' and Cetti's warblers' body fat decreased. Pied flycatchers were fatter during the main migration period (Figure 3.6).

Table 3.6. GLMM for fat score in response to the random factor year, the fixed factor age and the covariate time, during autumn migration. The test is adjusted (Type I error).

			Fat score P-values[a]			
Effects	Bluethroat	Cetti's warbler	Chiffchaff	Reed warbler	Willow warbler	Pied flycatcher
Year	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Time	0.766	**0.000**	**0.029**	**0.000**	**0.000**	**0.002**
Age	**0.000**	**0.033**	**0.000**	**0.000**	0.388	0.109
Age*Time	0.518	**0.032**	**0.000**	0.204	**0.024**	0.407
N adults	267	451	2057	2496	53	78
N 1-year	704	7403	5465	10413	606	566

[a] P-value = level of significance

Table 3.7. Seasonal average fat score at first capture.

	Autumn			Spring		
Species	N[a]	Mean Fat score ± SE	One-Way ANOVA	N[*]	Mean Fat score ± SE	One-Way ANOVA
Bluethroat	977	1.98 ± 0.04		2	-	
Cetti's warbler	8752	1.93 ± 0.10		8	-	
Chiffchaff	9342	2.27 ± 0.01	P=**0.000**	31	2.68 ± 0.16	
Reed warbler	12938	2.96 ± 0.01		651	3.08 ± 0.04	P=**0.000**
Willow warbler	748	3.24 ± 0.05		832	3.31 ± 0.03	
Pied flycatcher	646	3.58 ± 0.05	F=1078,85	224	1.98 ± 0.07	F=77.85

[a] includes all captures – adults, 1-year birds and birds of unknown age.

Table 3.8. Mean fat score comparison between early, main and late migrants during autumn migration.

Species	Early		Main		Late		ANOVA
	N	Mean±SE	N	Mean±SE	N	Mean± SE	P[a]
Bluethroat	66	2.03 ± 0.12	845	1.97 ± 0.04	66	2.11 ± 0.12	0.608
Cetti's Warbler	601	2.10 ± 0.04	7387	1.94 ± 0.01	764	1.65 ± 0.03	**0.000**
Chiffchaff	842	2.44 ± 0.03	7577	2.26 ± 0.01	923	2.21 ± 0.03	**0.000**
Reed Warbler	785	2.39 ± 0.04	10890	2.93 ± 0.01	1263	3.64 ± 0.04	**0.000**
Willow Warbler	75	3.19 ± 0.11	616	3.23 ± 0.06	57	3.32 ± 0.17	0.863
Pied Flycatcher	64	3.05 ± 0.17	553	3.66 ± 0.05	29	3.14 ± 0.23	**0.000**

[a] level of significance

During spring migration trans-Saharan species showed significantly different average fat scores with Willow warblers carrying more fat than Reed warblers and Pied flycatchers, respectively (Table 3.7). Chiffchaffs, the only short/medium-distance migrant analysed, showed similar mean fat score than Reed warblers (Tamhane test: *p*=0.114) but none of the species fat score variation was influenced by time of capture

(Table 3.9). No seasonal body mass variation was detected for neither of the species. Size, on the contrary, contributed to body mass variation in all species, and particularly for Pied flycatcher, this variation was influenced also by the interaction of size with time of capture.

Table 3.9. Analysis of covariance for body mass in response to the covariates wing and time during spring migration. The test is adjusted (Type I error).

	P-values[a]							
Factor/ Variable	Chiffchaff		Reed warbler		Willow warbler		Pied flycatcher	
	Body mass	Fat score	Body mass	Fat score	Body mass	Fat score	Body mass	Fat score
Wing	**0.040**	-	**0.000**	-	**0.000**	-	**0.000**	-
Time	0.833	0.385	0.088	0.129	0.363	0.136	0.073	0.206
Wing*Time	0.941	-	0.101	-	0.791	-	**0.045**	-
N	31	31	646	651	826	832	222	224
R²	0.148	0.026	0.340	0.004	0.255	0.003	0.145	0.007

[a] P-value = level of significance

Pied flycatchers were the only species that fat stores tended to increase towards the end of the pre-breeding migration period (Figure 3.6 and 3.7). Fat scores of the other species, on the contrary, decreased during the season. Body mass increased for all species except for Willow warblers, that similarly to fat score, were lighter towards the end of season.

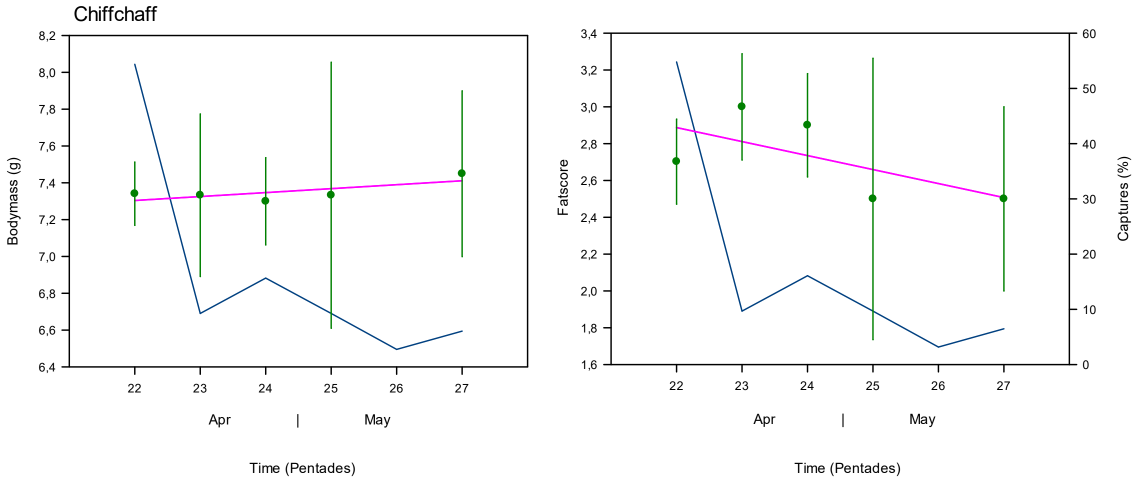

Figure 3.6. Seasonal distribution (line plots; both columns), mean body mass ± SE (dots, left column) and fat score ± SE (dots, right column) variation of Chiffchaffs during spring migration at Canal Vell. In pink, regression line for all data on plot of the dependent variable (body mass or fat score) with time.

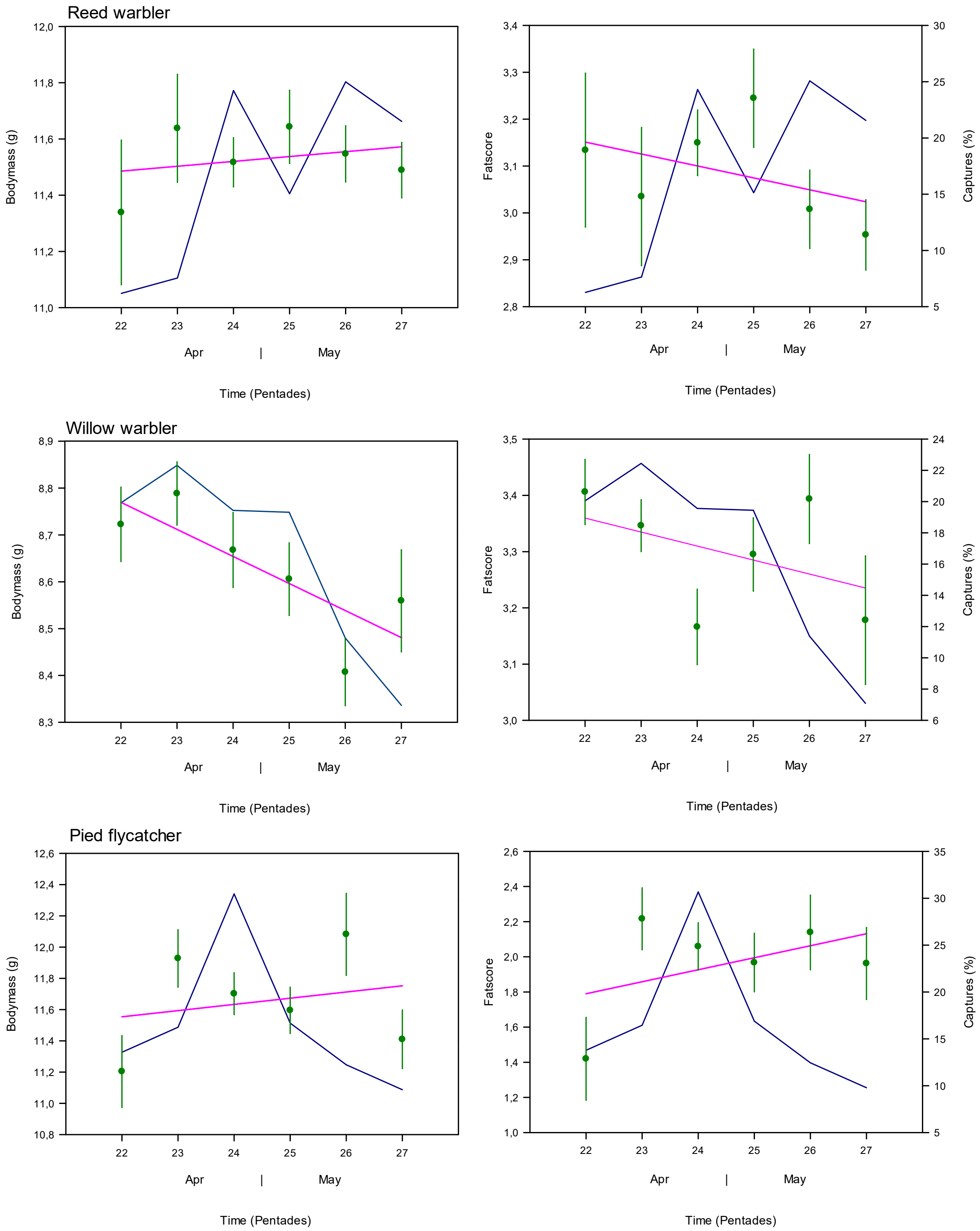

Figure 3.7. Seasonal distribution (line plots; both columns), mean body mass ± SE (dots, left column) and fat score ± SE (dots, right column) variation of trans-Saharan species during spring migration at Canal Vell. In pink, regression line for all data on plot of the dependent variable (body mass or fat score) with time.

Comparison between migration seasons

Trans-Saharan migrants were caught in substantial numbers during both seasons allowing seasonal comparison. Willow warblers and Pied flycatchers were significantly heavier in autumn than in spring. Reed warblers tended to be heavier in spring but not in a significant way. Fat scores were slightly higher in spring in Reed and Willow warblers, although significantly so only for Reed warblers, whereas Pied flycatchers were significantly leaner in spring than in autumn (Table 3.10).

Spring stopover for the studied Mediterranean wintering species was insignificant (very low captures for Cetti's warblers and Bluethroats) and only Chiffchaffs provided some data that was worth the analysis. Mean body mass was similar between spring and autumn, not so for fat score, and birds were fatter during spring than during autumn migration.

Table 3.10. Chiffchaffs, Pied flycatchers, Reed and Willow warblers mean body mass and fat score at first capture for autumn and spring migration seasons.

		Body mass				Fat score			
Species		N[a]	mean ± SE	t[b]	P[c]	N[a]	mean ± SE	t[b]	P[c]
Chiffchaff	spring	31	7.33 ± 0.12			31	2.68 ± 0.16		
	autumn	9301	7.37 ± 0.01	-0.331	0.741	9342	2.27 ± 0.01	2.21	**0.027**
Pied flycatcher	spring	222	11.67 ± 0.08			224	1.98 ± 0.07		
	autumn	639	14.60 ± 0.08	-26.27	**0.000**	646	3.58 ± 0.05	-17.54	**0.000**
Reed warbler	spring	646	11.54 ± 0.05			651	3.08 ± 0.04		
	autumn	12862	11.46 ± 0.01	1.59	0.112	12938	2.96 ± 0.01	2.87	**0.004**
Willow warbler	spring	827	8.66 ± 0.03			832	3.31 ± 0.03		
	autumn	742	9.01 ± 0.05	-5.44	**0.000**	748	3.24 ± 0.05	1.28	0.201

[a] Total number of birds with valid body mass and fat score values. This number is different from total number of birds captured.
[b] t-test
[c] level of significance

DISCUSSION

When and how well prepared are songbirds captured at Canal Vell?

Post-breeding migration.

Our study revealed that trans-Saharan species at Canal Vell come to pass ahead of Mediterranean wintering species, which agrees with the fact that the average migration speed (distance covered per day) in autumn is higher among tropical migrants than among migrants wintering in southern Europe (Ellegren 1993). This spatio-temporal segregation will eventually help to avoid the overlap in the use of the stopover area of similar species with different requirements competing for the same resources (Figure 3.1). The strong spatio-temporal segregation between the two *Phylloscopus* was already detected in the Iberian Peninsula (Onrubia and Telleria 2013). In addition, if the energy for flight is defined as accumulated fat, long-distance migrants also carried more fat than short to middle-distance ones (Table 3.7), as they are required to migrate faster and further. All six species showed different migration phenologies. Reed warblers were captured first, but their migration pattern was protracted until October, because adults migrated earlier than juveniles (Figure 3.4). It is important to remark that some of the early captures, mainly adults, may belong to the breeding populations of the Ebro delta (Fouces 2004). The other long-distance migrants migrate faster and in a more constrained way because they must cover large distances to reach their winter quarters and primarily are selected to maximize migration speed (Alerstam and Lindström 1990) (Figure 3.1). Short-distance migrants’ main flow takes place after the peak of migration of trans-Saharans, starting gradually from September onwards for Cetti’s warblers and Bluethroats and later in the season for Chiffchaffs. Moreover, Cetti’s warblers and Chiffchaffs were leaner at the end of season (Figure 3.3) certainly because late birds may be wintering in the Ebro delta or in the Mediterranean region, are near the end of migration and have less energetic requirements.

It is known that the phenology patterns may differ between age groups (eg. Jakubas and Wojczulanis-Jakubas 2010, Harnos *et al.* 2015, McKinnon and Love 2018, Schmaljohann *et al.* 2018) and if we assume that commonly adult long-distance migrants start migration earlier than first-year birds, and contrariwise for short distance migrants (Berthold 2001), our results support this statement for Reed warblers (trans-Saharans) and also for Cetti’s warblers and Chiffchaffs (Mediterranean wintering species) (Tables 3.2 and 3.4). Young Cetti’s warblers carry on a post-breeding dispersion searching for more temperate wintering areas (Cantos 1992) leaving the breeding areas before adults. The 16 to 1 capture ratio between first-year and adult birds at our site helps to second it.

Different autumn migration patterns by sex were already described for Chiffchaffs (Geen 1988) but there is no evidence of the age differences and the interaction of both age and time of migration that we found in our study, with juveniles arriving earlier than adults, unless first-year birds were mainly females, as reported in a previously study at an inland site at south-east England (Geen 1988). Different age phenology patterns were also reported for Willow warblers for several sites along the Spanish mediterranean coast (Asensio and Cantos 1989), but we did not find this pattern at our site. However, for this particular species’ age patterns remain not very clear. Near its breeding grounds in Sweden, and due to post-breeding moult, adults arrive to stopover sites after first-year birds (Lindström *et al.* 1996). Later, through continental Europe, adults catch up with juveniles which migration speed suffers a slight retardation at the Mediterranean area (Hedenström and Pettersson 1987), as it seems to occur at our site. Migration continues further south-west (see Chapter 2) and adults probably overtake first-year birds and mix up with other birds from Great-Britain breeding populations, producing general intra-specific differences in the phenologies found in more southern stopover sites. A similar pattern occurs for Bluethroats with adults migrating significantly faster than juveniles near the breeding grounds but then juveniles increase migration speed as the autumn progress (Ellegren, 1990). Once in Iberia, no differences between ages are found (Correia, 2013). Finally, although Harnos *et al.* (2015) pointed out that in the Carpatian Basin, juvenile Pied flycatcher migrate 4 days earlier on average than adult birds, no evidence of a different age pattern of migration was found at our site. These results may indicate that, except for species that breed in more southern places (like Reed Warblers) usually both ages reach the stopover sites in the Mediterranean region simultaneously.

Differential migration has been put forward not only for phenology patterns but also regarding body condition (eg. Jones *et al.* 2002). At our site, adult Mediterranean wintering birds were heavier than juveniles but only adult Bluethroats and Chiffchaffs were fatter, and this agrees with other similar findings, at least for Bluethroats (Ellegren 1991, Arizaga 2011). In this case, differences in weight seem to be related to fat accumulation, as adults with a relatively high capacity for efficient foraging or due to superior feeding conditions associated with age differences in seasonal timing of migration, may achieve a faster rate of fat deposition (Alerstam and Lindström 1990).

Adult Reed warblers were heavier than juveniles, but in contrast to other studies, carried in average less fat (Jakubas and Wojczulanis-Jakubas 2010), what is contrary to the accepted theory of time-selected migration strategy and may evince size differences between ages affecting body mass. But also, Reed warblers are common breeders at our site and most adults leave the area already in August, before juveniles, that continue using our site until November. After leaving, adults still have time to refuel along the migration route before crossing the Mediterranean. First year birds, migrating later, are more time constraint and fat levels increase with the progress of season (Figure 3.4) to improve speed of migration and try to reach their wintering quarters successfully. Therefore, the progress of season may determine some amount of variation in body condition. It is not the same to be at the beginning of the journey than at the end, and birds must adapt to different habitat scenarios and requirements throughout the entire migration period. In fact, late Reed warblers, mostly juveniles, were fatter as they have more way to do in less time, whereas Mediterranean wintering species like Cetti's Warblers and Chiffchaffs had lower fat scores towards the end of migration as they were closer to their winter quarters (Figure 3.3). Late migrants, however, had higher body mass. This shows that the differences in weight can reflect fat stores variation (more fat accumulated more weight) like in Reed warblers, but in some other species, like Cetti's warblers and Chiffchaffs these differences may be the result of the interaction of other factors like flight muscle changes (Marsh 1984, Lindström *et al.* 2000, Bauchinger and Biebach 2005), changes in the size of internal organs (Bauchinger *et al.* 2005), differences in body water content (Karlsson *et al.* 1988, Lundgren *et al.* 1995) or in the overall size of birds.

In the case of Cetti's warblers, the size variation could be also the result of differences on age (adults being larger than juveniles) or sex (Bibby and Thomas 1984). Age differences in size were also reported for Willow warblers (Norman 1983, Asensio and Cantos 1989), male Bluethroats (Ellegren 1991), Reed warblers (Peiró 2003) as well as sexual size dimorphism for Chiffchaffs (Catry *et al*. 2005). Therefore, taking in account size was necessary to evaluate temporal body mass variation properly and to eliminate any size effects that could affect it. After controlling for size, time of migration still influenced body mass and fat scores for all trans-Saharan migrants and Cetti's warblers. Only Bluethroats and Chiffchaffs, both wintering in the Mediterranean and without nearby breeding populations, showed similar average weight throughout migration although late Chiffchaffs were leaner, especially first-year birds (Figure 3.3).

All trans-Saharan migrants tended to increase fat scores towards the end of autumn, paralleling the body mass general trend (Figure 3.4). Unlike these species, later Cetti's warblers seemed to carry less fat and this agree with the expected body condition of birds preparing for wintering and without high energetic migration requirements. Pied flycatchers instead, were in better body condition during the peak of migration showing that these birds still had some amount of travel before end up on their winter quarters. If their migration strategy is to prioritise overall time of migration this could explain their rather fast passage (Figure 3.1) maintaining some amount of energy to keep going. If the stopover area has poor feeding availability or is not located before an ecological barrier birds will have, nevertheless, enough energy to execute these subsequent hops.

Pre-breeding migration.

During spring migration, the sequence of passage reverses and Mediterranean wintering species leave to their breeding grounds up north before the incoming of trans-Saharan migrants, as we see by their very low capture rates. In fact, Chiffchaffs, with only 31 captures in 5 years, left the site before the main passage period of long-distance migrants (Figure 3.2). Willow warblers were the first species to stopover with more intensity and carried in average more fat than the other trans-Saharans, nevertheless they showed a negative trend of body condition throughout spring (Figure 3.6). They were followed by Pied flycatchers and finally Reed warblers, whose captures increased towards the end of the season, probably due to the arrival of future breeding birds in the area. Pied flycatchers were in average leaner than the other species, probably because they arrive fat depleted after crossing the Sahara in a non-stop flight directly from their winter quarters in Africa (Ouwehand and Both 2016). It is possible that populations from different breeding origin may arrive to our site as supported by the correlation found between size of birds and time of capture, showing that birds with different sizes have different time of passage (Table 3.9). Moreover, it was the only species that improved its body condition with the progress of season (Figure 3.6). Chiffchaffs and Reed warblers showed similar fat score what could indicate similar migration strategies. Both species may be not "truly" Mediterranean wintering or trans Saharan, respectively, and some studies reveal that for instance, Reed warbler individuals from Central and Northern Europe have started to wintering on the Mediterranean coast (Nieto *et al.* 2018) and that Chiffchaffs can perform longer migrations and winter in sub-Saharan grounds (Moreno-Opo *et al.* 2015).

Our site is an important stopover area during return migration for Willow warblers with more captures in spring than in autumn. All the other species were present with more strength in autumn. The existence of circular routes called *loop migrations* (Berthold

2001), recently proved for some trans-Saharan migrants (Schmaljohann *et al.* 2012, Kristensen *et al.* 2013, Koleček *et al.* 2016, Klvaňa *et al.* 2018) and already suggested for Willow warblers (Pearson and Lack 1992), could explain the variation between spring and autumn intensity of passage. The increase in the number of spring captures of Willow warblers at our site could be the result of the presence of birds from the British breeding populations that adopt a more direct return route from their winter quarters (Norman and Norman 1986) compared with a more southwestern route adopted in autumn. Moreover, the geographical location of the Ebro delta, in the fastest route to reach their breeding grounds, supports this theory. A pattern of counter-clock wise loop migration was also reported previously for Pied flycatchers (Pilastro *et al.* 1998, Ouwehand 2016) although in our area the annual number of captures was a little bit higher in autumn.

It is also important to remark that: a) the pre-breeding ringing period (from 15th April to 15th May) does not cover the entire species’ passage as in the case of Reed warblers (Telleria *et al.* 1999) and b) the Mediterranean-wintering species leave before most of the trans-Saharan migrants arrive (Finlayson 1981). The enlargement of the actual pre-breeding ringing period would be desirable for better understanding of spring migration and the annual life cycle of short-distance migrants and birds that winter or breed at our site.

Autumn vs spring: two different seasons, two different ways?

It was expected that, in autumn, birds would be in better condition just before crossing a geographical barrier and leaner in spring due exactly to the opposite cause. This was true only for Pied flycatchers. Willow warblers were heavier in autumn, but fat stores were similar in both seasons what gives support to the theory of loop migration for this species. Different populations, probably with different overall sizes, use our site in different seasons. Lower body mass in spring may be the result of losing water contents after crossing the Sahara Desert and the Mediterranean Sea. Reed warblers weighed similarly in both seasons but were fatter in spring, being closer to a time-selected model of migration (accumulate enough fat to stopover less times), as pre-breeding migration needs to be faster. Robson *at al.* (2001) proposed Reed warblers as time-minimising migrants during spring in North-eastern Spain. Nevertheless, higher fat scores during spring may indicate that probably birds come from closer wintering quarters (Nieto *at al*. 2018) as we see also for Chiffchaffs with higher fat scores during spring.

Final remarks

Stopover decisions and, therefore, total time of migration may be dependent on when birds perform migration and how fit they arrive to the stopover areas along their migration route. It would be expected that birds of different migration status (short or long-distance migrants) and therefore in different stages of migration, as well as birds during spring or autumn migration, showed different condition at arrival.

During autumn, trans-Saharan species occur at Canal Vell before the Mediterranean wintering species due to higher average migration speed of the long-distance migrants. The spatio-temporal segregation avoids the overlap of similar species in the stopover area, and it has its maximal expression in the time of passage of the two *Phylloscopus* species. Long-distance migrants carried more fat than short to middle-distance as they are required to migrate faster and further.

All six species showed significantly different phenologies. The sequence of migration at Canal Vell was:

Reed Warblers→Willow warblers→Pied Flycatcher→Cetti's warblers→Bluethroats→Chiffchaffs.

Reed warblers' migration pattern was protracted due to age differences and to birds from the local breeding population. The other long-distance migrants migrate faster and maximize migration speed. Short-distance migrants arrive later in the season and they prepare to winter as supported by the decrease of fat scores of Cetti's warblers and Chiffchaffs at the end of season.

Age differences in phenology patterns found for Reed warblers, Cetti's warblers and Chiffchaffs agree with the theory that adult long-distance migrants start migration earlier than juveniles, but vice versa for short distance migrants. For Chiffchaffs there are no references of the age differences reported in this study. Willow warblers and Pied flycatchers, although showing differential migration near the breeding grounds, both ages arrive toghether to our site.

At Canal Vell, although adult mediterranean wintering birds were in average heavier than juveniles, only adult Bluethroats and Chiffchaffs showed higher fat scores and in this particular case, differences in weight seem to be related to fat accumulation. Adults are more efficient in foraging or due to differences on timing of arrival find better feeding conditions at the stopover area. In the case of the trans-Saharan species, adult Reed warblers carried less fat than juveniles what is opposite to the accepted theory of time-selected migration. The fact that Reed warblers are common breeders at our site may explain this difference as probably a high number of adult breeding birds start migration carrying less fat as they still have time to refuel along the migration route before crossing the Mediterranean.

The progress of season is responsible of some amount of variation in body condition. For trans-Saharan migrants, late birds are expected to be fatter because they have less time to finish migration, as we found for Reed warblers. On the other hand, Mediterranean wintering species are closer to their winter quarters and should show lower fat scores towards the end of migration, like we found for Cetti’s warblers. Pied flycatchers are trans-Saharan migrants but were in better body condition during the peak of migration what could explain their rather fast passage.

During spring migration, Mediterranean wintering species leave to their breeding grounds before trans-Saharan migrants arrive, in the following sequence:

Chiffchaffs→Willow warblers→Pied flycatchers→Reed Warblers

Willow warblers carried in average more fat than the other trans-Saharans but with a negative trend of body condition throughout the season. Pied flycatchers arrived fat depleted possibly after crossing the Sahara in a non-stop flight. Chiffchaffs and Reed warblers, with similar fat score, may be in an intermediate stage between being a long and short distance migrant as there is evidence that Reed warblers from Central Europe may winter on the Mediterranean coast and Chiffchaffs winter in sub-Saharan areas (Moreno-Opo *et al.* 2015).

Our site is an important stopover area for Willow warblers during pre-breeding migration, with more influx of this species in this period, what confirms the existence of a loop migration for this species. All the other species, certainly due to mortality at wintering grounds, had more captures during autumn, although for Pied flycatchers both seasons were similar. Pied flycatchers were leaner in spring than in autumn, as expected after crossing a geographical barrier. Willow warblers, however had similar fat stores in both seasons. The fact that Willow warblers were heavier in autumn may be a sign the existence of a loop migration and birds caught in spring and in autumn may be from different populations or that they lost water contents or suffered changes in internal organs after crossing a geographical barrier. Reed Warblers and Chiffchaffs were fatter in spring, as expected for time-selecting migrants.

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CHAPTER IV

Should I stay, or should I go: extrinsic and intrinsic factors influencing stopover decisions of songbirds with different migration strategies in the Ebro Delta.

INTRODUCTION

Songbird migration between breeding and wintering grounds consists of successive periods of flight and stopover. The time migrants spend landed is seven times longer than the time they spend flying (Hedenström and Alerstam 1997) since birds must balance the energy slowly accumulated during stopover and quickly lost during flight (Akesson *et al.* 1995). Is the variation of total stopover duration, but not the travel speed, the general biological mechanism of regulating total speed of migration (Schmaljohann and Both 2017; Schmalljohann *et al.* 2017). Consequently, the knowledge of the factors involved in the necessary resting time between flight bouts is very important to completely understand the temporal and spatial organization of the migration phenomena and could be used to identify suitable stopover areas and design effective conservation strategies for migratory songbirds (Berthold 2001, Sheehy *et al.*2011).

The stopover of birds during migration chiefly entails two components: time, i.e. stopover duration, and energy, defined as fuel deposition rate (FDR). Both components may be influenced by environmental factors like habitat, topography, predation and food availability, competition and weather aloft, and intrinsic factors, like energy stores, body mass at arrival, moult, progress of season, time of day and time programme (Jenni and Schaub 2003). Moreover, the refuelling rate affects the length of stopover and both components exercise as selective pressures described in well-known theories of optimal migration (Alerstam and Lindström 1990, Lindström and Alerstam 1992, Weber et al. 1994, 1998, Hedenström 2008, Alerstam 2011). FDR is also related to the suitability of the stopover area, as food availability is its most common limiting factor and may

provide a relatively simple alternative proxy of habitat quality (Lindström 2003), defining the role of a specific area in the migration route of songbirds. In this chapter, we will evaluate how some environmental (extrinsic) and intrinsic factors influence the components of stopover and shape the specific migration behaviour of six passerine species with different migration behaviour (trans-Saharan and Mediterranean wintering species) at the Ebro delta, during both periods of the annual migration cycle.
We will also study differences in stopover length and FDR among species with different migration behaviours, as well as specific differences between age classes related to both migration components. For instance, younger birds are often less skilled foragers (Wunderle 1991) and are usually socially subordinate to adults (Gauthreaux 1978). Therefore, socially dominant migrants appear to gain an advantage in food acquisition, which should translate into an increased rate of refuelling and/or shorter length of stopover (Moore *et al.* 2003). FDR is positively correlated with dominance status and this fact may be important for the spatial and temporal pattern of migration in birds that compete for resources at stopover sites (Lindström *et al.* 1990).

Within the intrinsic factors involved in stopover, we will focus on the body condition of birds at arrival and their endogenous time programme. Lean birds are expected to stay longer than fat birds (Cherry 1982, Yong and Moore 1997, Seewagen and Guglielmo 2010, Cohen 2014), stopover length and FDR vary with the progress of season (Balança and Schaub 2005) and late migrants have higher fuel stores (Schaub and Jenni 2000a), higher FDR (Schaub and Jenni 2000b) and seem to travel at a higher speed (Ellegren 1993, Fransson 1995).

Our results will be considered in the light of the optimal migration strategy theories already described elsewhere (Alerstam and Lindström 1990, Lindström and Alerstam 1992, Weber 1994, Klaassen and Lindström 1996, Hedenström and Alerstam 1997, Weber and Houston 1997, Alerstam and Hedenström 1998, Hedenström 2008, Alerstam 2011). Finally, the significance of the Ebro delta as a suitable stopover area for songbirds with different migration strategies will be discussed.

STUDY AREA AND METHODS

To perform the study, we analysed ringing data collected during both autumn (1992-2000) and spring (1996-2000) songbird migration at Canal Vell, a coastal lagoon surrounded by large extensions of flooded reed bed and some shrub areas in the Ebro Delta, NE Spain (UTM 31T 4512629 N; 313110 E) (see Chapter 2). Data were collected in a standardized way following the European-African Songbird Migration Network manual of field methods (Bairlein 1995). First trapped birds were ringed and aged according to Svensson (1992) and Jenni and Winkler (1994). Weight was recorded using an electronic scale, to the nearest 0.1mm and fat classes were scored from 0 to 8 following Kaiser (1993). It was also registered the time of capture (to the nearest h) for each bird.

The study approached six different passerine species with different migration strategies, three Mediterranean wintering migrants (MW): the Bluethroat (*Luscinia svecica*), the Cetti's warbler (*Cettia cetti*) and the Chiffchaff (*Phylloscopus collybita*); and three trans-Saharan migrants (TS): the Pied flycatcher (*Ficedula hypoleuca*), the Reed warbler (*Acrocephalus scirpaceus*) and the Willow warbler (*Phylloscopus trochilus*). Reed warbler's captured before the 24 of august were excluded from the analysis to avoid breeding birds in the area (Cramp 1998, Schaub and Jenni 2001a).

For each species, we analysed the total data set and four other data subsets in relation to age (adult and first year birds) and body condition defined by fat score. Birds below the median specific fat score were defined as lean birds and birds equal or above this median as fat birds.

Stopover duration

The time passerines spend stopping over can be estimated by different methods using capture-recapture data. The method of the minimum stopover length or duration (MSD), where stopover duration is calculated as the difference between the dates of last and first capture, is being used to calculate time birds spend landed during migration since the 1960s (Szulc-Olech 1965, Bairlein 1985, Moore and Kerlinger 1987, Morris 2005). This is a conservative approach of the stopover duration estimation and appears to be highly biased because actual arrival and departure dates are unknown and only the data subset of birds trapped twice is used. Furthermore, as birds caught only once are the majority, this measure does not represent the entire population (Schaub *et al.* 2001a, Chernetsov 2012). In the search of the real stopover duration, other methods have been tested using capture-mark-recapture analysis, firstly to estimate the probabilities of birds staying at the site after last capture (Lavée *et al.* 1991, Kaiser 1995) and secondly to calculate both probabilities of birds being in the population after and before its capture (Schaub *et al.* 2001a). More recently, Schaub's method has been discussed (Efford 2005, Pradel *et al.* 2005) and some authors started not to include recruitment analysis into the total stopover duration estimation (Salewski *et al*. 2007, Bayly and Rumsey 2007, Chernetsov *et al*. 2007, Chernetsov 2010) because it may be biasing the estimation high as it is excluding individuals that arrive and depart before the estimated time of arrival (Efford 2005). Nevertheless, in favour of comparison with other studies that use Schaub's method to perform stopover analysis on the same species studied here or with other data from the Ebro delta and to establish a line of arguments, we adopted this approach for stopover length estimation at our site.

The estimation of real stopover duration (RSD) was done using the software SODA, a method developed and described by Schaub *et al.* (2001). The method consists on an analysis of capture-mark-recapture data with Cormack-Jolly-Seber (CJS) models. These models allow the estimation, for birds present at the site at time *i*, of the probabilities of having been at the site already at time *i*-1 by means of a recruitment analysis (Pradel 1996) and the probability of still being at the site at time *i*+1 by means of a survival analysis (Lebreton *et al.* 1992). The sum of the recruitment analysis (time spent before capture) and the survival analysis (time spent after capture) estimations reflect the total stopover duration.

Analysis of recruitment and survival were based on the individual capture stories (including birds caught only once) which were pooled over five days (pentades), according to the fixed-date pentade system proposed by Berthold (1973) and commonly used in similar studies. After pooling the data, we assessed the goodness-of-fit (GOF) of a global CJS model with the software U-CARE 1.4 (Choquet *et al.* 2002) to consider if there was a significant deviation of the data from the model. In the case of a significant deviation, we examined the four sub-tests provided by U-CARE to detect systematic deviations from the expected values. These deviations may be the result of the occurrence of birds that stopover only for one day, commonly called transients (Pradel *et al.* 1997) or by trap-dependence (trap-happiness or trap-shyness) of the birds (Pradel 1993).

Another possible cause for the lack of fit of the data in the absence of systematic deviations is overdispersion (when data exhibit more variation than expected). To estimate de degree of overdispersion of our data we calculated the variance inflation factor $\hat{c}$ as the quotient of the residual deviance and the residual degrees of freedom from the goodness of fit test (Burnham and Anderson 1998). $\hat{c}$ was calculated up to a significance level of P=0.10 of the goodness of fit tests; beyond this value it was assumed to be 1. In our case, overdispersion may be due to a lack of independence between individuals, as birds migrate in groups, or heterogeneity in capture probability between individuals (Schaub and Jenni 2001a). If the pooled data did not fit the CJS model or evidenced the presence of transients, we assessed year by year GOF tests to identify which years showed transience problems or overdispersion. These years were then eliminated from the total sample and a new GOF test was performed with the new data set. When the presence of transients was still evident after eliminating problematic years, we decided to use the original pooled data set with a model taking account of transients.

GOF tests were significant for autumn data sets and subsets of Cetti's Warblers (except adults), Reed Warblers (except adults) and Pied Flycatchers (except fat birds). Years 1993 and 1995 of Cetti's Warblers main data set didn't fit the model and were removed from the analysis. Even so, the results still showed the presence of transients (subtest 3SR significant, Pradel *et al.* 1997). Consequently, we decided to maintain the original pooled data and fit the transient model instead. A similar decision was made for Pied Flycatchers. In the Reed Warblers case, we found the presence of transients only in the pooled data and we decided, from the beginning, to apply the transient model. Only for adult Cetti's Warblers we excluded three problematic years (1992, 1998 and 2000) to fit the CJS model.

After choosing a first general model that fit our data, we used the program SURGE 5 (Pradel and Lebreton 1993) to fit predefined models to the data for the recruitment and survival analysis. For data sets that fit the CJS model, we analysed four different models of recruitment and survival: $(\gamma/\phi_t, p_t)$, $(\gamma/\phi_t, p)$, $(\gamma/\phi, p_t)$ and $(\gamma/\phi, p)$ with γ for probability of recruitment, ϕ for probability of survival, p for probability of recapture and t for time. In the other hand for data that fit the transient model (Pradel *et al.* 1997) we applied another four different models taking in account of transients. The chosen models were $(\gamma/\phi_{a2t}, p_t)$, $(\gamma/\phi_{a2t}, p)$, $(\gamma/\phi_{a2}, p_t)$ and $(\gamma/\phi_{a2}, p)$, with a_2 for two age classes, newly (transients) and previously marked birds (retrapped). We calculated for each model the modified Akaike Information Criterion (QAICc) which accounts for overdispersion and sample size (Burnham and Anderson 1998), and the smallest QAICc was chosen to estimate stopover duration. Models differing less than 7 in QAICc from the best model were used also as second-best models.

The results of the GOF of the most general model – the CJS model – for all species as well as the best recruitment and survival models selected are shown in Tables 4.1 (autumn migration) and 2 (spring migration).

Table 4.1. Results of the goodness-of-fit for the Cormack-Jolly-Seber model calculated with U-CARE and models of recruitment and survival selected with SURGE 5.0, for data sets (total) and subsets (adults, first-year birds, fat and lean birds) of all species in autumn migration. The models were used to calculate stopover duration. $\hat{C}$ is the variance inflation factor (χ^2/df) and is indicated when the data is overdispersed. P=level of significance. n=sample size.

						Models Selected	
Specific data sets	χ^2	*df*	*P*	$\hat{C}$	*n*	Recruitment	Survival
Bluethroat							
Total	58.1	59	0.510		1022	(γ, p)	(ϕ, p)
Adults	12.9	32	0.999		307	(γ, p)	(ϕ, p_t)
First year	37.2	51	0.926		708	(γ, p)	(ϕ, p)
Fat	34.5	46	0.996		558	(γ, p)	(ϕ, p)
Lean	14.2	44	0.999		461	(γ, p)	(ϕ, p)
Cetti's Warbler							
Total	491.0	222	0.000	2.21	9237	(γ_{a2t}, p)	(ϕ_{a2}, p_t)
Adults	54.1	32	0.750		840	(γ_t, p)	(ϕ, p)
First year	342.6	210	0.000	1.63	7541	(γ_{a2t}, p_t)	(ϕ_{a2}, p_t)
Fat	367.5	186	0.000	1.98	5439	(γ_{a2},p_t)	(ϕ_{a2}, p_t)
Lean	246.7	161	0.000	1.53	3719	(γ_{a2}, p_t)	(ϕ_{a2}, p_t)
Chiffchaff							
Total	52.2	44	0.190		9706	(γ_t, p)	(ϕ, p_t)
Adults	11.1	19	0.920		2293	(γ_t, p)	(ϕ_t, p)
First year	31.2	35	0.650		5554	(γ_t, p)	(ϕ, p_t)
Fat	36.9	33	0.290		4863	(γ_t, p)	(ϕ, p_t)
Lean	22.2	32	0.900		4734	(γ_t, p_t)	(ϕ, p_t)
Pied Flycatcher							
Total	17.4	7	0.015	2.49	648	(γ_{a2}, p)	(ϕ_{a2}, p)
Adults	-	-	-	-	78	-	-
First year	16.8	5	0.005	3.36	567	(γ_{a2}, p)	(ϕ_{a2}, p)
Fat	4.4	3	0.223	1.45	384	(γ_t, p)	(ϕ, p)
Lean	8.5	2	0.014	4.26	262	(γ_{a2}, p)	(ϕ_{a2}, p)
Reed Warbler							
Total	144.8	71	0.000	2.04	9339	(γ_{a2}, p_t)	(ϕ_{a2}, p_t)
Adults	10.7	16	0.828		840	(γ_t, p)	(ϕ, p)
First year	130.1	71	0.000	1.83	8414	(γ_{a2t}, p)	(ϕ_{a2t}, p)
Fat	80.2	60	0.042	1.34	5486	(γ_{a2}, p_t)	(ϕ_{a2}, p)
Lean	82.6	59	0.023	1.40	3818	(γ_{a2}, p_t)	(ϕ_{a2}, p_t)
Willow Warbler							
Total	20.0	23	0.640		749	(γ, p_t)	(ϕ_t, p)
Adults	0.00	1	1.000		54	(γ, p)	(ϕ, p)
First year	16.0	22	0.820		609	(γ, p_t)	(ϕ_t, p)
Fat	13.1	17	0.730		396	(γ_{t}, p)	(ϕ, p)
Lean	5.4	15	0.990		351	(γ, p_t)	(ϕ, p)

Table 4.2. Results of the goodness-of-fit tests for the Cormack-Jolly-Seber model calculated with U-CARE and models of recruitment and survival selected with SURGE 5.0, for data sets (total) and subsets (adults, first-year birds, fat and lean birds) of all species in spring migration. P=level of significance. n=sample size.

					Models selected	
Specific data sets	χ^2	*df*	*P*	*n*	Recruitment	Survival
Pied Flycatcher						
Total	0.00	1	1.000	225	(γ, p)	(ϕ, p)
Fat	0.00	0	0.000	125		
Lean	0.00	1	1.000	100	(γ, p)	(ϕ, p)
Reed Warbler						
Total	3.56^{E-24}	5	1.000	737	(γ, p)	(ϕ, p)
Fat	0.00	2	1.000	458	(γ, p)	(ϕ, p)
Lean	0.00	4	1.000	278	(γ, p)	(ϕ, p)
Willow Warbler						
Total	1.70^{E-23}	1	1.000	836	(γ, p)	(ϕ, p)
Fat	1.00	0	1.000	468	(γ, p)	(ϕ, p)
Lean	0.00	0	0.000	367		

After identifying the best models for the immigration and the emigration processes, we estimated mean stopover duration and its precision by bootstrapping, using the software SODA 1.11 (Schaub *et al.* 2000). The bootstraps were run with 1000 resamplings, because increasing the number of resamplings to 10000 in the bootstrap would have no effect on the estimation of the mean but decreases its precision slightly (Schaub and Jenni 2001a).

We analysed stopover duration between species, ages and body condition in a weighted analysis of variance. Estimates were log-transformed before analysis, and weights used were the inverse of the squared covariance ($1/cv^2$). Usually, estimates are weighted by the squared standard error, but the variable estimated here is duration and consequently a positive number, so the standard error is typically proportional to the value of the estimate.

Finally, we compared RSDs obtained with the program SODA with the specific MSDs, calculated as the difference in days between last and first capture plus one entire day (night migrants arrive the night preceding first capture and depart the night after last recapture).

Fuel Deposition Rate (FDR).

We assumed that the FDR of a bird is the average change in body mass per day, calculated as the difference between body mass at first capture and last recapture during the same migration season divided by the number of days between these two capture events. However, as birds were captured and weighed at different time of day, we first adjusted body mass data with respect to time of capture, its square (to model a non-linear curve) and size (wing length). The estimates for these adjustments were derived from a linear model with body mass as dependent variable and time of capture, its square and wing length as independent variables. After adjusting body mass values, we calculated specific lean body mass (LBM), i.e. the body mass of a bird carrying no migratory fat, for birds with the same wing length group (in this case, length of P8) by linear regression of body mass and fat score (Ellegren and Fransson 1992). Finally, FDR was calculated as the proportion of lean body mass (LBM)/day to allow inter-specific comparisons, following the formula:

$$FDR\ (g\ d^{-1}) = \frac{abm_{LC} - abm_{FC}}{(d_{LC} - d_{FC})]} / LBM,$$

where *abm* is adjusted body mass, *d* is day and *FC* and *LC* stands for first and last capture.

Specific FDR was compared using the one-way analysis of variance (ANOVA), followed by a post-hoc test for multiple comparisons. To compare groups (age and body condition) in the same species, we used the independent samples t-test, preceded by the Levene's test for equality of variances. The one-sample t-test was used to analyse if mean FDR differed from zero.

Autumn migration stages were defined as early, main and late migration following Chapter 3 of this thesis. Further, FDR on the three migration stages were compared using the one-way analysis of variance (ANOVA) followed by a post-hoc test for multiple comparisons. In spring, due to reduced time span, the migration stage was time measured in pentades instead of the three stages considered in autumn data analysis.

To reduce handling effects on body condition, we excluded all birds (spring and autumn) retrapped the day after capture (Schaub and Jenni 2000b). In addition, for autumn migration data analysis, to avoid locally born birds not yet on migration or that started wintering at the area, we established (based in our results, see Figure 4.4) that stopovers larger than 13 days were also excluded. We applied the same method for spring migration, to exclude mainly breeding Reed Warblers at our site.

To conclude, we also tested the effect on FDR of three distinct factors: species, status (MW vs. TS migrants) and season (autumn or spring), with three different General Linear Models (GLM) of covariance analysis (ANCOVA). The first model (Model I), ran with autumn and spring data separately, tested the factor species including the covariates size (length of P8), migration stage (early, main and late migration), body condition (at arrival) and minimum stopover duration (MSD). The second model (Model II), ran with only autumn data, tested the factor status with size, migration stage, body condition and MSD as covariates and the third model (Model III), ran with only TS migrants' data, tested the factor season with the covariates size, body condition and MSD. We used Type I sum of squares, where the effect of a variable is evaluated only after adjustment for the ones entered previously.

RESULTS

Stopover duration estimations

Stopover length of Cetti's Warblers during post-breeding migration increased greatly towards the end of season, as we could expect from a regular wintering species at our site (Rivaes 2011). The same occurred with Chiffchaffs, although the stopover started to increase only since the middle of the season with the arrival of the bulk of wintering birds (see Chapter 3), when birds showed lower stopover duration. Willow warblers and Chiffchaffs, two morphologically similar species with different migration behaviours, seemed to show the same stopover duration pattern, but with lower average stopover length for the trans-Saharan species (Figure 4.1).

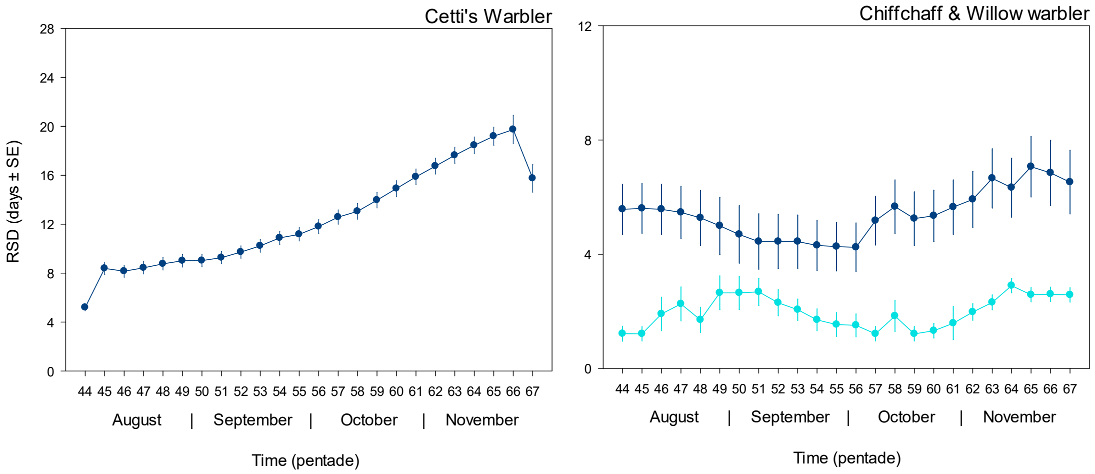

Figure 4.1. Autumn seasonal variation of real stopover durations for Cetti's warblers, Chiffchaffs (dark blue) and Willow warblers (light blue).

However, Willow warblers used our site for stopover during the first half of the autumn migration period avoiding the presence of Chiffchaffs, which arrived later to the area (see Chapter 3). The main bulk of Willow warblers (pentade 46 to 56) showed longer stopovers than early and late ones, although towards the end of the season, very late migrants showed even longer stopovers. Stopover for this trans-Saharan species was in average short, between one and three days only.

The stopover estimation models chosen for Bluethroats, Reed Warblers and Pied Flycatchers were not time dependent (Table 4.1), so stopover estimations showed constancy in time during all season, and both trans-Saharan migrants stopped over less time than the Mediterranean wintering one (Table 4.3).

Table 4.3. Average autumn stopover durations obtained with the program SODA (mean values of 24 capture occasions ± SE)

	Estimations of real stopover duration (days)				
Species	Total	Adults	First-year	Fat	Lean
Cetti's Warbler	12.42±0.61	17.99±3.40	11.31±0.62	12.81±0.81	11.88±0.93
Bluethroat	5.65±0.64	6.86±1.71	5.43±0.70	7.07±1.20	4.33±0.62
Chiffchaff	5.41±0.95	2.89±0.63	6.01±1.37	5.09±1.20	6.05±1.92
Reed Warbler	3.16±0.14	2.60±0.17	3.02±0.53	2.57±0.17	3.78±0.22
Pied Flycatcher	2.48±0.85	-	2.74±0.98	1.65±0.68	1.95±0.86
Willow Warbler	1.98±0.38	1.41±0.71	2.02±0.43	1.67±0.35	2.40±0.69

Autumn stopover length was species specific (weighed ANOVA: $F_{5,139}$=269.21, p=0.000). Cetti's Warblers had the highest stopover duration followed by Bluethroats, Chiffchaffs, Reed Warblers, Pied Flycatchers and finally Willow Warblers (Table 4.3).

During autumn, Mediterranean wintering birds spent more time landed than trans-Saharan migrants (7.82±0.48 days and 2.54±0.07 days, respectively; weighed ANOVA, $F_{1,143}$=539.56, p=0.000).

Three species showed significant age differences in stopover length during post-breeding migration. Adult Cetti's warblers stopped over longer than first-year birds (weighed ANOVA: $F_{1,47}$=9.07, p=0.004), but the other way around for Chiffchaffs (weighed ANOVA: $F_{1,47}$=107.95, p=0.000) and Willow warblers (weighed ANOVA: $F_{1,47}$=16.43, p=0.000). Adult and first-year Reed warblers had similar average stopovers but used our site in different time moments (see Chapter 3). For both age classes late migrants stopped over longer (Figure 4.2). Bluethroat stopover estimations were time constant (Table 4.1) and throughout the post-breeding migration period adults stopped over longer than first-years, but not in a significant way (Table 4.3). During autumn only first-year Pied Flycatchers data was available.

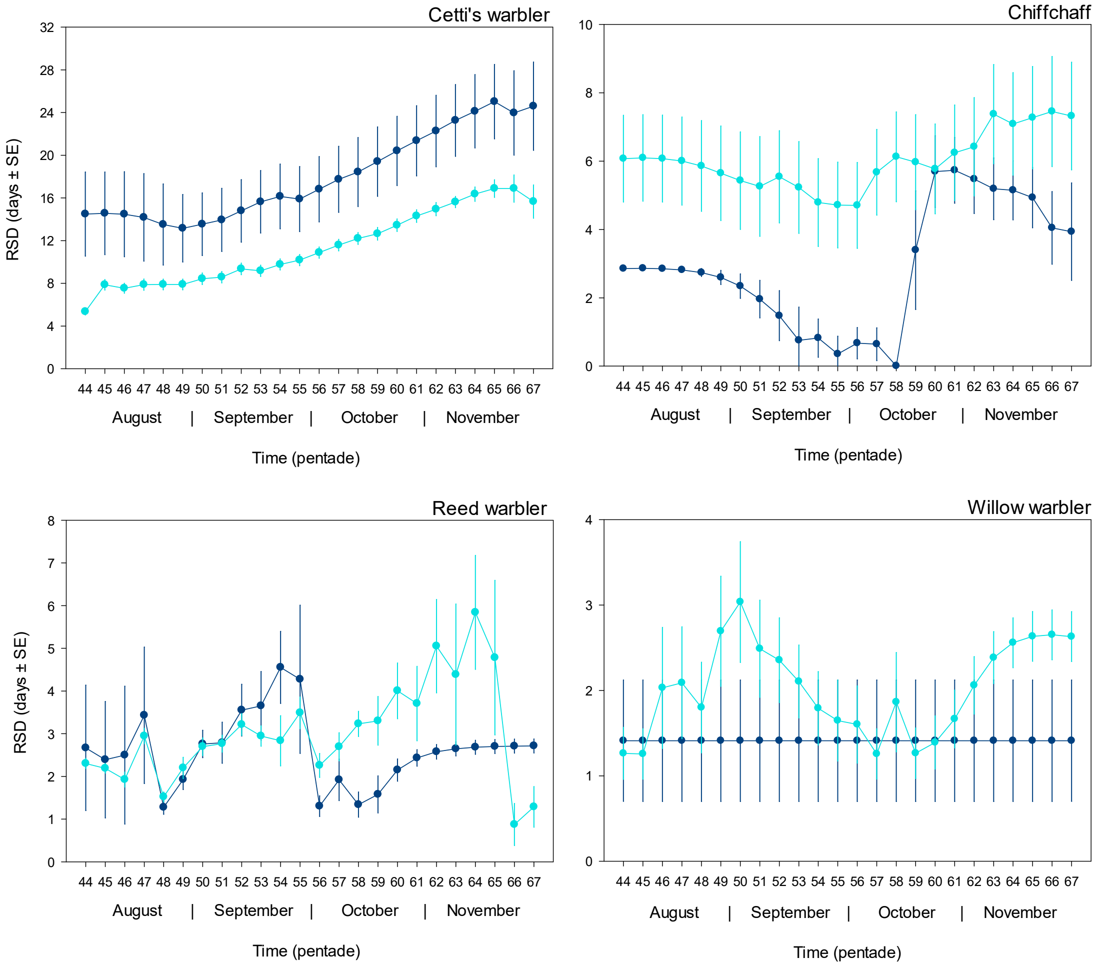

Figure 4.2. Autumn seasonal variation of real stopover durations of adult (dark blue) and first-year (light blue) birds for Cetti's warblers, Chiffchaffs, Reed warblers and Willow warblers.

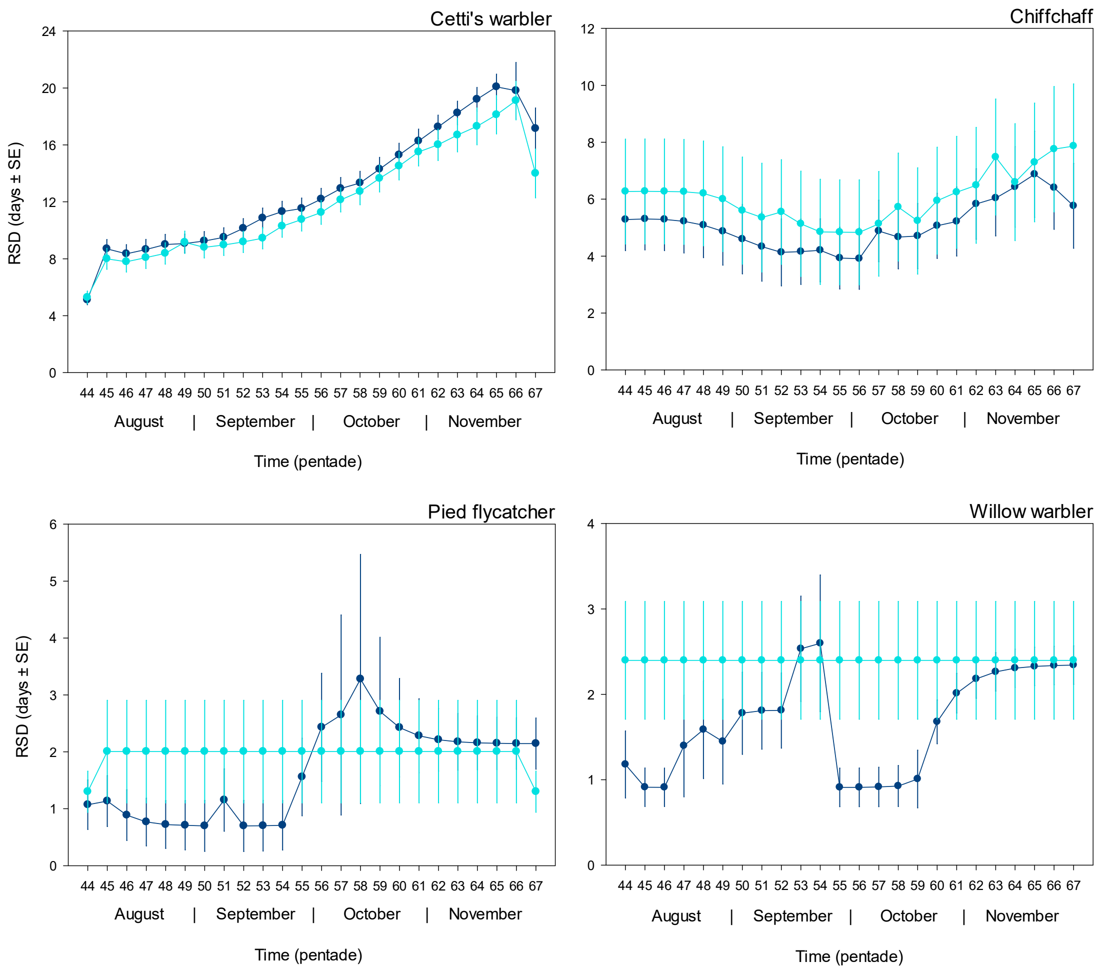

Figure 4.3. Autumn seasonal variation of real stopover durations of fat (dark blue) and lean (light blue) Cetti's warblers, Chiffchaffs, Pied flycatchers and Willow warblers.

Stopover lengths during spring migration were significantly different between the three trans-Saharan species (weighed ANOVA: $F_{2,16}$=194236.60, p=0.000). Reed Warblers stopover longer than Pied Flycatchers and Willow Warblers, respectively (Table 4.4). Lean Reed Warblers stopped significantly longer than fat birds, as well (weighed ANOVA: $F_{2,16}$=4738756.00, p=0.000), but standard error for the average stopover length of lean birds was high. Pied Flycatchers and Willow Warblers body condition comparisons were not performed because of very low recapture rates.

When comparing both migration periods in general, autumn stopover of trans-Saharan migrants was significantly longer than in spring (2.54±0.07 days and 0.94±0.18 days, respectively; weighed ANOVA, $F_{1,90}$=322.43 p=0.000).

Table 4.4. Average spring real stopover duration obtained with the program SODA (mean value for all 6 capture occasions ± SE)

	Stopover duration (days)		
Species	Total	Fat	Lean
Pied Flycatcher	0.46±0.10	-	0.57±0.14
Reed Warbler	2.01±1.90	0.45±0.05	5.41±30.68
Willow Warbler	0.35±0.08	0.33±0.13	-

Stopover durations estimated by the MSD method corroborate the fact that Mediterranean wintering migrants stopped over longer than trans-Saharans (Table 4.5). RSD estimations were considerably lower than MSD estimations for all species during both migration periods (Figure 4.4).

Table 4.5. Values of stopover duration estimated by the method of the minimum stopover duration [mean ± SE (sample size)].

Species	Minimum Stopover Duration	
	Autumn	Spring
Bluethroat	16.45±1.32 (82)	
Cetti's Warbler	14.48±0.33 (1173)	
Chiffchaff	9.62±0.50 (320)	
Pied Flycatcher	7.50±2.28 (8)	3.20±0.42 (10)
Reed Warbler	8.48±0.23 (847)	5.67±0.85 (21)
Willow Warbler	7.73±0.83 (66)	3.54±0.62 (13)

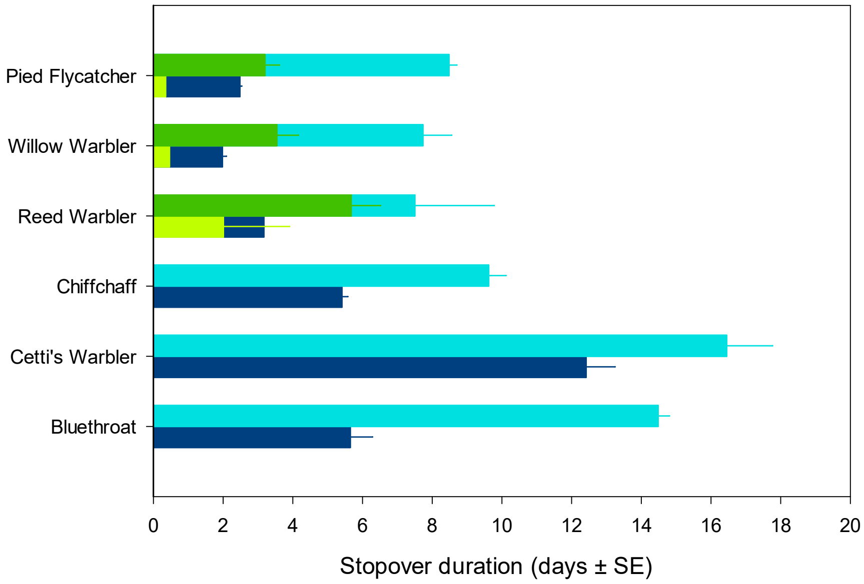

Figure 4.4. Real Stopover Duration (under bars) vs Minimum Stopover Duration (upper bars) during autumn migration (blue bars) and spring migration (green bars).

Fuel deposition rate (FDR) estimations

FDR differed between species during autumn (one-way ANOVA: $F_{5,1533}$=13.01 p=0.000) (Figure 4.3). Only Reed and Willow warblers in general refuelled at our site and the other species showed negative or null fuel deposition rates (Table 4.6). It is important to remark that Pied flycatcher's sample was very low with only four recaptures and the results of the analysis of this species may not be accurate.

Only Bluethroats showed significant age differences in fuel load deposition (independent samples t-test: t_{35}=2.33, p=0.026). Fuel deposition rates in autumn were similar to zero for adults of all species, as well as for first-year Chiffchaffs and Pied flycatchers. Otherwise, juvenile Bluethroats and Cetti's warblers, both Mediterranean wintering species, lost fat during stopover while juvenile Reed and Willow warblers increased it. Cetti's warblers, Chiffchaffs and Reed warblers with different body condition showed significant different FDR (independent samples t-test: $t_{657.874}$=6.20, p=0.000; $t_{104.085}$=3.10, p=0.003; $t_{535.613}$=2.08, p=0.038, respectively). Both lean Reed and Willow warblers fat load increased during stopover while fat Cetti's warblers and Chiffchaffs showed negative fat deposition rates (Table 4.6).

Table 4.6. Fuel deposition rates (mean±SE % of lean body mass/day) of all species total data sets and subsets (age and body condition) during autumn migration. Sample size is shown (between brackets). Bold values mean significant difference from zero (one-sample t-test).

	Fuel Deposition Rate				
Species	Total	Adults	First year	Lean	Fat
Bluethroat	-0.32±0.20 (37)	0.35±0.27 (11)	**-0.60±0.24** (26)	-0.13±0.26 (20)	-0.54±0.30 (17)
Cetti's Warbler	**-0.26±0.05** (724)	-0.28±0.16 (48)	**-0.22±0.06** (603)	0.05±0.07 (378)	**-0.64±0.09** (346)
Chiffchaff	**-0.81±0.21** (178)	-0.60±0.32 (40)	-0.58±0.31 (100)	-0.19±0.17 (98)	**-1.57±0.41** (80)
Pied Flycatcher	-0.83±1.69 (4)	-	-0.83±1.69 (4)	-0.41±2.32 (3)	-2.07 (1)
Reed Warbler	**0.31±0.11** (565)	0.99±0.90 (22)	**0.28±0.11** (543)	**0.54±0.14** (284)	0.08±0.17 (281)
Willow Warbler	**1.72±0.70** (31)	1.07±1.37 (5)	**1.85±0.80** (26)	**2.83±0.87** (15)	0.68±1.04 (16)

When comparing both migration periods in general, autumn stopover of trans-Saharan migrants was significantly longer than in spring (2.54±0.07 days and 0.94±0.18 days, respectively; weighed ANOVA, $F_{1,90}$=322.43 p=0.000).

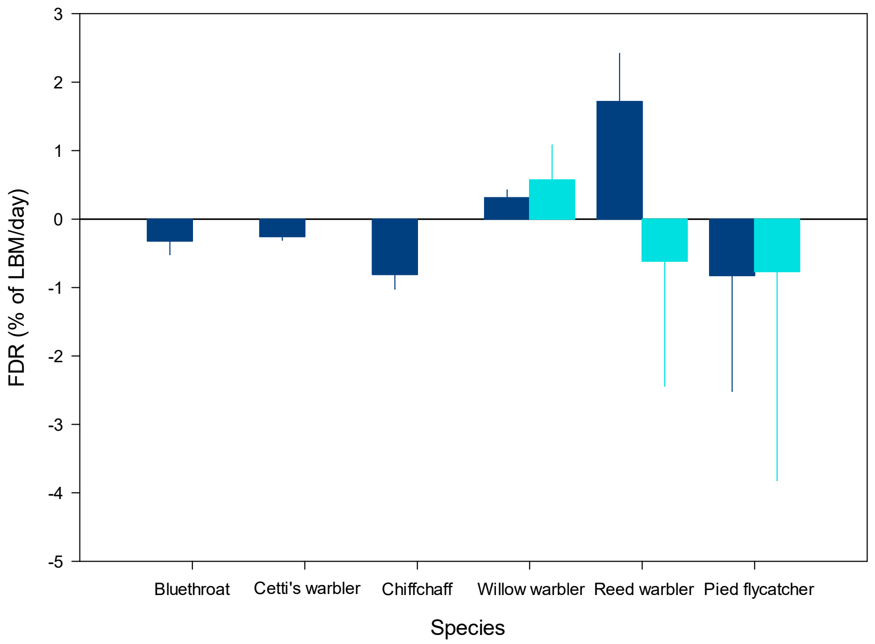

Figure 4.5. Total fuel deposition rates (mean±SE % of lean body mass/day) of each species during autumn and spring stopover at the Ebro delta.

During spring stopovers, none of the species gained nor lost weight (one-way ANOVA: $F_{2,17}$=0.32 p=0.729, Table 4.7, Figure 4.5). All four Pied Flycatchers recaptured were lean birds. Lean Reed Warblers showed positive FDR and fat ones negative, and the opposite occurred for Willow Warblers, but the differences were not significant (independent samples t-test: t=1.69 p=0.131 and t=0.43 p=0.738, respectively) nor the values were different from zero.

Table 4.7. Fuel deposition rates (mean±SE % of lean body mass/day) of species data sets and subsets during spring migration. Sample size is shown (between brackets).

	Fuel Deposition Rate		
Species	Total	Lean	Fat
Pied Flycatcher	-0.77±3.06 (4)	-0.76±3.08 (4)	-
Reed Warbler	0.57±0.51 (11)	0.99±0.66 (8)	-0.44±0.52 (2)
Willow Warbler	-0.61±1.83 (5)	-1.84±4.92 (2)	0.32±0.99 (3)

Results of the GLM analysis showed that FDR during autumn stopovers was significantly correlated with size, migration stage, body condition at arrival and MSD. The factor species was, as expected, an important source of FDR variation as well as the interactions body condition*MSD and body condition*species (Table 4.8, Model I-

Autumn). However, the percentage of variation of the variable explained by the model was low (Adjusted R^2=0.122). On the other hand, there was no significant correlation of FDR with any covariant or factor during spring migration (Table 4.8, Model I-Spring), and the factors and variables of the model explained only the 17% of the variation of the response variable (Adjusted R^2=0.174).

Table 4.8. Significance levels (*P*-values) for three different General Linear Models of covariance analysis for FDR in response to distinct factors and variables. Model I (Autumn and Spring): factor species and covariates size, migration stage, body condition and MSD (minimum stopover duration). Model II (only autumn): factor status (MW birds vs TS migrants) and covariates size, migration stage, body condition and MSD. Model III (only TS birds): factor season (spring vs autumn) and covariates size, body condition and MSD. -: factors or variables not used in the model. The test is adjusted (Type I error).

Dependent variable: Fuel Deposition Rate				
Factors/ Variables	Model I (Autumn)	Model I (Spring)	Model II	Model III
size	**0.000**	0.837	**0.000**	0.780
migration stage	**0.017**	0.429	**0.018**	-
body condition	**0.000**	0.552	**0.000**	**0.000**
body condition*migration stage	0.197	0.476	0.202	-
MSD	**0.000**	0.103	**0.000**	**0.000**
MSD* migration stage	0.862	0.557	0.863	-
MSD* body condition	**0.008**	0.374	**0.009**	0.954
Species	**0.000**	0.686	-	-
Species* body condition	**0.000**	0.966	-	-
Species* MSD	0.831	0.059	-	-
Status	-	-	**0.000**	-
Status* body condition	-	-	**0.001**	-
Status* MSD	-	-	0.542	-
Season	-	-	-	0.410
Season* body condition	-	-	-	0.606
Season* MSD	-	-	-	0.051
Adjusted R^2	0.122	0.174	0.105	0.042

During autumn migration at our site, Mediterranean wintering birds lost weight (-0.36±0.06 % LBM/day) and showed a negative trend all over the season, while trans-Saharans increased weight daily (0.38±0.11 %LBM/day) and the difference between these two groups was significant (one-way ANOVA: $F_{5,1533}$=13.00 p=0.000). Trans-Saharan migrants started migration losing weight during stopover but afterwards FDR significantly increased toward late birds. Early and late migrants showed statistically different fuel loads (Tamhane test: p=0.030, Figure 4.6).

FDR, as well as their body condition at arrival, varied for birds with different migration behaviour. GLM analysis showed that FDR was correlated with the factor status as well as with the interaction of this factor with body condition at arrival, although the variance explained by the model was low (Adjusted R^2=0.105, Table 4.8, Model II).

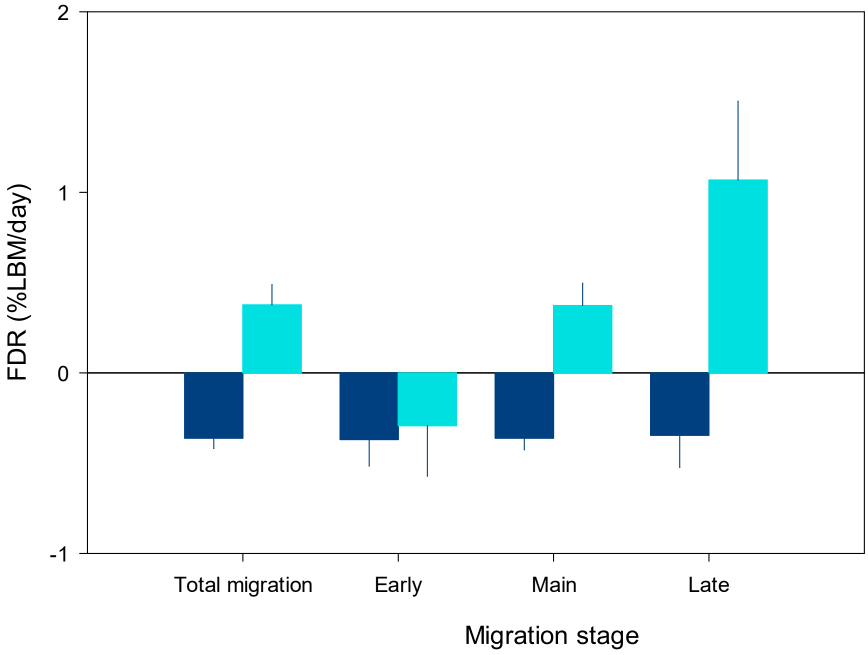

Figure 4.6. Fuel deposition rates of trans-Saharan migrants (light blue) and Mediterranean wintering species (dark blue) for total autumn migration period and during three different stages of migration.

Trans-Saharan migrants showed positive FDR during both seasons (autumn: 0.38±0.11 %LBM/day; spring: 0.01±0.75 %LBM/day), but the difference was not significant (independent samples t-test, t_{618}=0.59, p=0.556). Furthermore, FDR in spring was similar to zero. The GLM model results showed also that FDR was not correlated with migration season (autumn or spring) nor with interactions of covariates with this factor although only 4.2% of the variation of the dependent variable was explained by the model (Table 4.8, Model III).

DISCUSSION

Unlikely stated in other similar stopover studies, at our site migrant songbirds had estimated real stopover durations considerably shorter than those obtained with the minimum stopover duration method (Schaub *et al.* 2001, Rguibi-Idrissi *et al.* 2003). In fact, it is commonly accepted that stopover length calculated with the MSD method is usually underestimated, and real stopovers are actually much longer (Schaub *et al.* 2001), because the method only includes birds recaptured at least twice, without taking into account time spent at stopover before the first and after the last capture. But then, if the true stopover length of most birds is rather low but some of them stay a long time, are caught shortly after arrival and just before departure or by the end of the season (as in the case of Mediterranean wintering species), this would inflate MSD calculations (Schaub *et al.* 2001). Moreover, if stopover estimations are made without taking into consideration transients (birds that stop only for one or two days) and their proportion is high as it seems to occur at our site, this may lead to an overestimation of the overall mean stopover duration instead (Chernetsov 2012) and to avoid this artefact, we calculated RSD by fitting models that took account of transients after GOF tests were significant. We think that both arguments may be applied to explain our results, on one hand the presence of a high number of transients with stopovers of less than 2 days (in the case of trans-Saharan migrants) and on the other, birds that were already wintering at our site or nearby (Mediterranean wintering migrants).

Few studies analyse the stopover ecology of middle to short-distance songbird migrants or even compare it with long-distance migrants. Some of them show, however, that during spring middle-distance migrants have slightly longer stopovers (Bolshakov *et al.* 2000) and short-distance migrants usually accumulate less fat than long-distance migrants (Bairlein and Gwinner 1994). In Canal Vell, during autumn, we found that stopovers were longer for Mediterranean wintering species than for trans-Saharan migrants. Although stopover length was species specific, all long-distance migrant species stayed at our site between two and four days, while the species wintering in the Mediterranean area stayed more than five days. Furthermore, Cetti’s warblers and Chiffchaffs, species that usually winter at our site, showed longer stopovers towards the end of the season that combined with null or negative refuelling rates indicate that part of the individuals of these species may end migration in the Ebro delta or at other areas nearby (Bairlein 1985). Trans-Saharans instead, with shorter stopovers, showed positive fat deposition rates that increased towards the end of the season as expected for birds that are in a rush to get to their winter quarters and minimize time during migration. This is supported by the evidence that the progress of season spurs migratory fuel deposition both in caged birds and in the field during autumn (Dänhardt and Lindström 2001, Schaub and Jenni 2000b).

Birds in the field do not usually attain theoretical maximum fat deposition rates (Biebach 1996). For passerines the estimated mean rate of fat deposition is considered to be 2.4% of LBM/day (Alerstam and Lindström, 1990) and during autumn at our site trans-Saharan species showed in average, a much lower refuelling rate (Table 4.6). If the number of migrants was composed mainly of transients, i.e. birds which stopover for very short periods and were not refuelling, it probably means that:

i) the site was not a staging site, where the threshold of optimal fat deposition was not achieved, and birds only rested between flight bouts adopting a time minimization migration strategy (Alerstam and Lindström 1990), and/or

ii) they are not facing a great barrier and instead they are adopting a hopping strategy until they reach the final site before crossing the Mediterranean Sea (Warnock 2010, Schmaljohann et al. 2012), and/or

iii) The site habitat does not reach the threshold of landscape suitability for refuelling (Ktitorov *et al*. 2008).

In the first case, if our site was not a suitable fattening area (Basciutti *et al*. 1997) or birds had detected some predation risk or disturbance, we should expect a negative or very low FDR since perceived predation along the flyway may force birds to postpone the final fuel accumulation to the last stopover along the flyway (Chudzinska *et al*. 2016), what takes us to the second case. Trans-Saharan migrants stopping over at our site are not in front of a barrier but just moving along the coast (Elgea and Arizaga 2016). If birds did not reach a hypothetic endogenously programmed minimum FDR, needed to ensure necessary refuelling, instead of losing time and possibly weight too, they are likely to move on. Schaub and Jenni (2001b) already found very low average fattening indexes for Reed Warblers and Pied Flycatchers during autumn in the Ebro Delta and if the rate of fat deposition hinge on the extent to which specific nutritional needs can be fulfilled (Bairlein 1990, Biebach 1996) our site for some reason seems to offer low food availability or the predation risk is too high to forage efficiently. However, if at our site birds are not facing an ecological barrier, there is no need for refuelling at higher rates and the time they spent on stopover is not related to food availability but only with maintaining enough energy to reach the following stopover site and like this, minimizing also the total energy cost of migration including costs of energy transport and existence costs as well (Hendenström and Alerstam 1997).This is called the global update rule for time minimization (Huston 1998).

Finally, in the third case, Ktitorov *et al*. (2008) showed that in sites with less than 10% of woody habitat cover, birds tend to lose body mass or to gain mass at a lower rate. Their results reveal that in the case of Canal Vell at the time of their study, the woody habitat cover was only ca. 3% within a radius of 5km, and it did not change significantly during our trapping period. Nevertheless, in the case of birds that are specialist foragers in reed this rule may not apply.

During spring, the pattern recurred and trans-Saharan species with lower FDR had shorter stopovers, although the birds did not gain nor lose weight (Table 4.7), most likely because they were more predisposed to arrive quickly to the breeding grounds in what is a clearly driven time minimization strategy. Low FDR was already found for Reed Warblers during spring migration in NE Spain where the stopover site was primarily an area to make a daytime break between two nights of migratory flights (Robson *et al*. 2001). Stopover was longer in autumn than in spring (Figure 4.4) for all species as expected because the speed of songbird homeward migration is higher than post-breeding migration (Tottrup *et al*. 2012, Nilsson 2013).

Mediterranean wintering species during autumn migration refuelled at much lower rate than trans-Saharan migrants or even showed negative rates (Table 4.6) and had longer stopovers. Instead of moving on these birds decided to stay, even with low refuelling rates, as they were not time pressed, because they were near their winter quarters.

The time birds spent landed in autumn (estimated as MSD) produced some variation on FDR but it is not possible to clearly relate FDR to stopover duration and there may be environmental and endogenous factors that affect both energy and time components of stopover (Table 4.8 – Models I, II and III). Intraspecific competition is known to be within the possible environmental factors that influence both components of stopover (see Jenni and Schaub 2003). First-year birds usually show longer stopovers than adults (e.g. Ellegren 1991, Rguibi-Idrissi *et al*. 2003) as we found also for trans-Saharan migrants at our site. On the contrary, for birds that were supposedly near the end of migration, adult longer stopovers were influenced by dominant and most experienced birds established already on their wintering quarters and forcing first-year birds to continue their search for other suitable wintering areas. Despite that and for Chiffchaffs in particular, the pattern was similar to trans-Saharan migrants. A possible explanation is that closely related Chiffchaff subspecies with different migration strategies may converge to our stopover site during migration. If an important part of these birds were from breeding populations in the Iberian Peninsula, they should migrate longer distances than individuals from northern breeding populations that winter in the Mediterranean basin (Pérez-Tris *et al.* 2003) and therefore they may adopt a similar strategy to trans-Saharan migrants.

Concerning FDR, and the fact that subordinate and less experienced birds were expected to refuel slowly than adults, our results were not supportive, and fat deposition did not fit on an established pattern of intraspecific competition. Only Bluethroats showed age differences in FDR what was already described by Ellegren (1991) in a stopover site in Sweden.

Other factors, apart from intraspecific competition, certainly shape the rate of fuel deposition during stopover, for example, endogenous factors like energy stores at arrival or the time programme, i.e., the progress of season. Moreover, we found that during autumn, refuelling relied in part upon these endogenous factors (Table 4.8 - Model I). Therefore, once in a suitable refuelling site, birds with significantly higher fat scores at arrival should have smaller stopovers than individuals with lower fat scores (Biebach 1985, Goymann 2010). At our site, fat trans-Saharan migrants plus Chiffchaffs stayed less time than lean birds, what supports the idea of the Ebro Delta as a refuelling site, although low fuel deposition rates as well as very short stopovers may suggest low food availability. Most likely is not a problem of habitat quality but maybe a question of the time minimizing strategy adopted by these species. In addition, lean trans-Saharan migrants had higher FDR than birds in better body condition. If we assume that refuelling must be higher in fat birds than in lean ones before crossing an ecological barrier (Schaub and Jenni 2001b), our site is not the last stop before crossing the Mediterranean Sea in autumn. This is supported by lean Willow warbles that showed higher FDR than the mean rate estimated for passerines, although they were the only group from all species analysed that refuelled at this rate. Furthermore, higher Reed warbler's FDRs were reported for southerly places in S Spain and N Africa (Schaub and Jenni 2000b) and also from Portugal (Bibby and Green 1981). Stopover behaviour of Bluethroats and Cetti's Warblers, both Mediterranean wintering species, was different and fat birds showed longer stopovers than lean ones because of dominant birds that started to settle in for wintering. Moreover, refuelling rates were also dependent of migration status and related to body condition at arrival (Table 4.8, Model II).

During spring, return migration was faster, more direct and with shorter stopovers, as already described in several studies (e.g. Nilsson 2013). Even though fat stores at arrival did not affect FDR of trans-Saharans in spring (Table 4.7 – Model I, spring), in the case of the Willow warbler, fat individuals showed higher FDR as expected when birds just crossed an ecological barrier (Loria and Moore 1990, Kuenzi *et al.* 1991), although sample size was very low, and values were not significantly different.

The other intrinsic factor involved in stopover dynamics is time programme (i.e. progress of season). Some literature states that stopover is in average longer in early than in late migration and other that stopover increases with season (e.g. Lavée *et al.* 1991, Balança 2005, Cohen 2014). In our case, and during autumn, late Cetti's Warblers, Chiffchaffs and Willow Warblers showed longer stopovers, although the last two species stayed longer also during its main passage period (Figure 4.1). Reed Warblers show differential migration by age with adults migrating earlier than first year birds (See Chapter 3) but longer stopovers coincided with the late birds of both ages. In general, it seems that at our site late birds stay longer. In the case of trans-Saharan migrants, and probably Chiffchaffs, if they spend more time in stopovers just before an ecological barrier as said before, the few ones that arrive late, instead of following the coast with several hops towards south Iberia, they probably make one or two bigger jumps or even try to cross the Mediterranean with a possible stopover in the Balearic Islands. In addition, it is known that the progress of season accelerates autumnal migratory fuel deposition in caged birds and in the field (Lindström *et al.* 1994, Fransson 1998, Schaub and Jenni 2000b, Dänhart and Lindström 2001). At our site, FDR increased for trans-Saharan species during the season and late birds refuelled faster than early ones, maybe preparing themselves for longer jumps or for the imminent Mediterranean crossover. This agrees with the findings that late-migrating individuals have higher fuel stores and higher FDR and seem to travel at higher speed (e.g. Ellegren 1993, Fransson 1995, Schaub and Jenni 2000a, b).

Final remarks

At Canal Vell, Mediterranean wintering species had longer stopovers than trans-Saharan migrants but RSD estimates resulted lower than the ones obtained from the MSD method. If the number of birds on transience at a stopover site is high and is not considered when using the RSD method, the results may be overestimated. To avoid this, we used models taking into account transients and RSDs were shorter than MSD estimates for all species. On the other hand, in the case of Mediterranean wintering species, MSDs could also be overestimated due to the presence of birds already wintering at our site. The exact stopover length is though something difficult to measure only with ringing data and it would be more realistic if other monitoring methods like telemetry or GPS markers were used. Nevertheless, in this last case the sample size would be much lower than using the all-time ringing method. Even if the RSD method results are not precise, ringing data analysis allows us to make interspecific comparisons within the stopover ecology analysis.

Trans-Saharan migrants adopted similar time minimization strategies during pre and post breeding migration although autumn stopovers were longer than spring ones, due to a more concentrated spring migration period. During autumn, FDR increased with season as usual in time minimizing migration strategies. Nevertheless, average FDR was low what could reflect low food availability, high predation risk, the fact that our site is not in front of an ecological barrier or a combination of these factors like in the global update rule for time minimization. Moreover, the lack of suitable habitat cover may result in a low average FDR. Also, during autumn Mediterranean-wintering birds accumulated fuel at a lower rate than trans-Saharan migrants probably because they were not time pressed.

Fuel deposition rates were affected in some degree by stopover duration, but other environmental and intrinsic factors could be also involved. Factors like interspecific competition, with young trans-Saharan migrants and young Chiffchaffs stopping over longer than adults. Chiffchaffs, probably birds breeding in the Iberian Peninsula, adopt a similar migration strategy as long-distance migrants. Adults from the other Mediterranean wintering species show longer stopovers. Despite the age differences on stopover duration, only Bluethroats show significantly different fuel deposition rates for adults and first year birds.

Both energy stores at arrival and the progress of season are intrinsic factors that influence stopover at least during autumn migration. Fat trans-Saharan migrants plus Chiffchaffs stay less time than lean birds, as described in other refuelling sites, and although fuel deposition rates were in general low, lean trans-Saharan migrants showed higher rates. Birds stopping over at Canal Vell are not in front of crossing an ecological barrier and they move south. At least birds from the bulk of migration because late trans-Saharan migrants stay longer and refuel faster changing from the strategy of several hops along the coast to maybe crossing the Mediterranean Sea with a possible stop in some Balearic Island. Finally, fuel deposition rates were different between trans-Saharan migrants and Mediterranean wintering birds.

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CHAPTER V

Tonight we fly: a day in the life of transient songbirds regarding body mass variation.

INTRODUCTION

Stopover is the essential event during bird migration to recover from the previous flight episode and to prepare and refuel for the next one. Therefore, to achieve the main objective of migration, that is, of birds to reach wintering or breeding quarters successfully, it is important to stopover in high quality sites, with high fuel availability and where the birds will be protected from predation and competition, that is, a place where fuel deposition rate (FDR) is high (Cormier *et al.* 2013). If FDR is a proxy of stopover site quality, to know the FDR of migrants in a specific stopover site may be used for conservation management purposes.

There are two main methods to estimate FDR during stopover that use ringing data: one is based on the body mass changes of birds captured at least twice (e.g. Winker *at al.* 1992, Schaub and Jenni 2000b, Rguibi-Idrissi *et al.* 2003, Moore *et al.* 2017)), although this method excludes flyers (Rappole and Warner 1976), also called transients (i.e. migrants that make one or two-day stopovers) and that normally form the main block of captures (Chernetsov 2012). The other method is supported by the diurnal mean mass change of samples of birds captured during the day (the hourly trend of the mean mass of the first captures) (Dunn 2001, Delingat *et al.* 2009, Seewagen *et al.* 2011). However, this method requires some assumptions: a) birds arrive at the stopover site near dawn after an all night's flight, what usually happens on en route stopovers which are not located before ecological barriers (Delingat *et al.* 2009) and b) time of capture is independent of the bird's mass at dawn, therefore a gain in average body mass of birds trapped for one day represents the average body mass gain of all transients in the area (Dunn 2000).

Some studies found that individuals of several species had net daily gains greatly exceeding those of recaptured individuals (Winker *et al.* 1992, Bonter *et al.* 2007).

In Chapter 4 we already estimated FDRs at our site with the first method and saw that the values were in general low, what could indicate that our site is not a suitable area for refuelling during several days but instead birds use it for rest between consecutive flight bouts. To support this statement, we estimated diurnal body mass changes of three trans-Saharan and three Mediterranean wintering species during autumn and spring stopovers and the possible factors that could affect this variation, such as age differences or body condition at arrival. Like in the previous chapters we will focus on possible differences between species with different migration behaviour or among birds at different migration stages. Finally, we will compare diurnal fuel deposition rates (dFDR) with the daily rates estimated in Chapter 4. Diurnal activity of transients will be assessed, to relate it with the estimations of diurnal body mass changes.

By the end of the day transients are prepared to leave the stopover site and usually start to take off around sunset (Schmaljohann *et al*. 2013, 2015) and keep leaving the site during the following hours (Müller *et al*. 2016). Although the start of migratory restlessness can be affected by both intrinsic and extrinsic factors (Eikenaar *et al*. 2016), if we assume that birds become restlessness late in the afternoon (Eikenaar *et al.* 2014), increase their probabilities of being captured and that the decision to take off for a long-distance flight depends in part on body condition (Sjöberg *et al.* 2017), a possible variation in weight around dusk could be a predictor of birds staying in or leaving our site. The energetic state of a bird in combination with food availability at a particular stopover site can affect its decision whether to migrate or not (Gwinner *et al*. 1988). The objective of this study is, then, to share some light on how transients behave when sedimented and help to identify suitable one-day stopover areas.

STUDY AREA AND METHODS

Birds were captured from dawn to dusk, during both annual migration periods, at the shores of Canal Vell Lagoon at the Ebro Delta (NE Spain, UTM 31T 4512629 N; 313110 E), a coastal lagoon surrounded by large extensions of flooded reed bed and some shrub areas (see Chapter 2 for more information about the stopover site).

Data were collected both in autumn (from 1992 until 2000) and in spring (from 1996 until 2000) following standardized ringing procedures (for more details see Spina *et al.* 1993 and Bairlein 1995).

Birds were ringed and aged according to Svensson (1992) and Jenni and Winkler (1994). Among other measurements, weight was recorded using an electronic balance, to the nearest 0.1 mm and fat classes were scored with an eight-level scale (Kaiser 1993). We also recorded the time of capture (to the nearest h) for each bird. Birds were released immediately after this procedure.

Study species are the same treated in previous chapters: Bluethroat (*Luscinia svecica*), Cetti's warbler (*Cettia cetti*) and Chiffchaff (*Phylloscopus collybita*), the three of them short/medium-distance migrants and wintering in the Mediterranean region, and Reed warbler (*Acrocephalus scirpaceus*), Willow warbler (*Phylloscopus trochilus*) and Pied flycatcher (*Ficedula hypoleuca*), three long-distance trans-Saharan migrants. Reed warblers captured before the 24th August were excluded from the analysis because probably they were breeding birds (Cramp 1998, Schaub and Jenni 2000a).

Time of capture was recoded to hours from dawn, and all regression plots comprehend the first thirteen hours of the day. We defined birds trapped at hour 12^{th} and 13^{th} as late afternoon captures and all birds trapped afterwards were grouped as captures at dusk, that is, after sunset.

We analysed birds captured only once in the season, and they were treated as transients (birds that stopover for one day). To determine body condition, birds with fat scores under the specific median were defined as lean birds and birds equal or above this median, as fat birds. Finally, we defined autumn migration stages in early, main and late migration (see Chapter 3).

Statistical Analyses

Diurnal activity distributions were compared between species using the Kruskal-Wallis non-parametric test for k independent samples followed by Mann-Whitney U post-hoc pairwise tests. To compare activity patterns between seasons we used the Kolmogorov-Smirnov test.

To estimate diurnal variations in body mass a regression model was used with body mass as dependent variable and time of capture, its square (in order to model a non-linear curve) and size (length of primary 8) as independent variables. Specific diurnal body mass changes during autumn migration were estimated for age, body condition (lean and fat birds) and migration stage (early, main and late birds). The factors age and migration stage were excluded from the spring analyses, because of possible ageing bias and of a short capture period, respectively. The resulting regression equations were plotted using the specific mean value of length of primary 8.

We tested the effects of six variables on body mass of the individual birds with a type I analysis of covariance (ANCOVA) where the effect of a variable is evaluated only after adjustment for the ones entered previously. We first adjusted for the variables size, time of capture and its square. Then we evaluated the effects of age (only for autumn data) migration stage, body condition and their interaction with time on body mass.

We calculated specific dFDRs as the mean diurnal body mass changes obtained with the regression models developed previously. Finally, we plotted specific mean dFDR for body condition during both seasons, age groups and migratory stages only during autumn. Comparisons among migratory stages were made using one-way analysis of variance (ANOVA) followed by a post-hoc test for multiple comparisons. We used the t-test for independent samples between age groups and body condition. Both tests were preceded by the Levene’s test for equality of variances.

To compare body mass and size of birds captured during late afternoon (i.e. during the two hours before sunset) and dusk (i.e. during the two hours after sunset) we used the Mann-Whitney U-test for independent samples, and we plotted the specific mean body mass values for each species and season. All statistical analyses were performed with SPSS 24.0 package (IBM Corp. Released 2016)

RESULTS

Diurnal activity patterns

Capture figures reflect well the diurnal activity of transients during stopover. In autumn all species were more active during the first three or four hours of daylight, only Chiffchaffs had the main peak of activity late in the afternoon (Figure 5.1). Patterns of activity were different among species (Kruskal-Wallis test, $\chi^2_{(5)}$ =1503,90 p=0.000).

Pairwise comparisons showed two groups with different activity patterns that come to light: one including Mediterranean wintering birds (Bluethroats and Cetti’s warblers) and the other, trans-Saharan migrants (Willow warblers and Pied flycatchers). For both groups captures peaked in the first hours of daylight but long-distance transients had also a considerable amount of captures in the central hours of the day. Chiffchaffs and Reed warblers differed in their patterns from the rest of the species (Table 5.1). Trans-Saharan species showed different activity patterns for both migration seasons (Reed warbler K-S test, D=25.5, *p*=0.000; Willow warbler K-S test, D=19.2, *p*=0.000; Pied flycatcher K-S test, D=12.8, *p*=0.000).

During spring Willow warblers and Pied flycatchers were considerably active during the central hours of the day with an almost inactive period before sunset, while Reed warblers were active mainly during the first five hours. Trans-Saharan migrants' diurnal activity pattern was different among species (Figure 5.1; Kruskal-Wallis test, $\chi^2_{(2)}$ =53.95 *p*=0.000). Matching post-breeding migration, Willow warblers and Pied flycatchers showed similar patterns. Reed warbler's activity pattern instead, was different, with a main peak of captures early in the morning.

Table 5.1. Results for post-hoc Mann-Whitney U test for pairwise comparisons for diurnal activity patterns (BT-Bluethroat, CW-Cetti's warbler, CC-Chiffchaff, RW-Reed warbler, WW-Willow warbler, PF-Pied flycatcher). Similar pairs are highlighted.

Pairwise comparisons	Mann-Whitney U	SE	Bonferroni adjusted significance
Autumn			
BT-CW	611.090	271.974	0.370
BT-RW	-1396.288	270.724	0.000
BT-WW	-2346.970	403.159	0.000
BT-PF	-2396.827	400.377	0.000
BT-CC	-4625.353	268.338	0.000
CW-RW	-785.198	121.493	0.000
CW-WW	-1735.880	322.500	0.000
CW-PF	-1785.737	319.016	0.000
CW-CC	-4014.262	116.079	0.000
RW-WW	-950.682	321.447	0.047
RW-PF	-1000.540	317.951	0.025
RW-CC	3229.065	113.120	0.000
WW-PF	-49.857	436.278	1.000
WW-CC	2278.383	319.440	0.000
PF-CC	2228.525	315.922	0.000
Spring			
RW-WW	-170.717	24.823	0.000
RW-PF	-180.083	37.100	0.000
WW-PF	-9.366	36.579	1.000

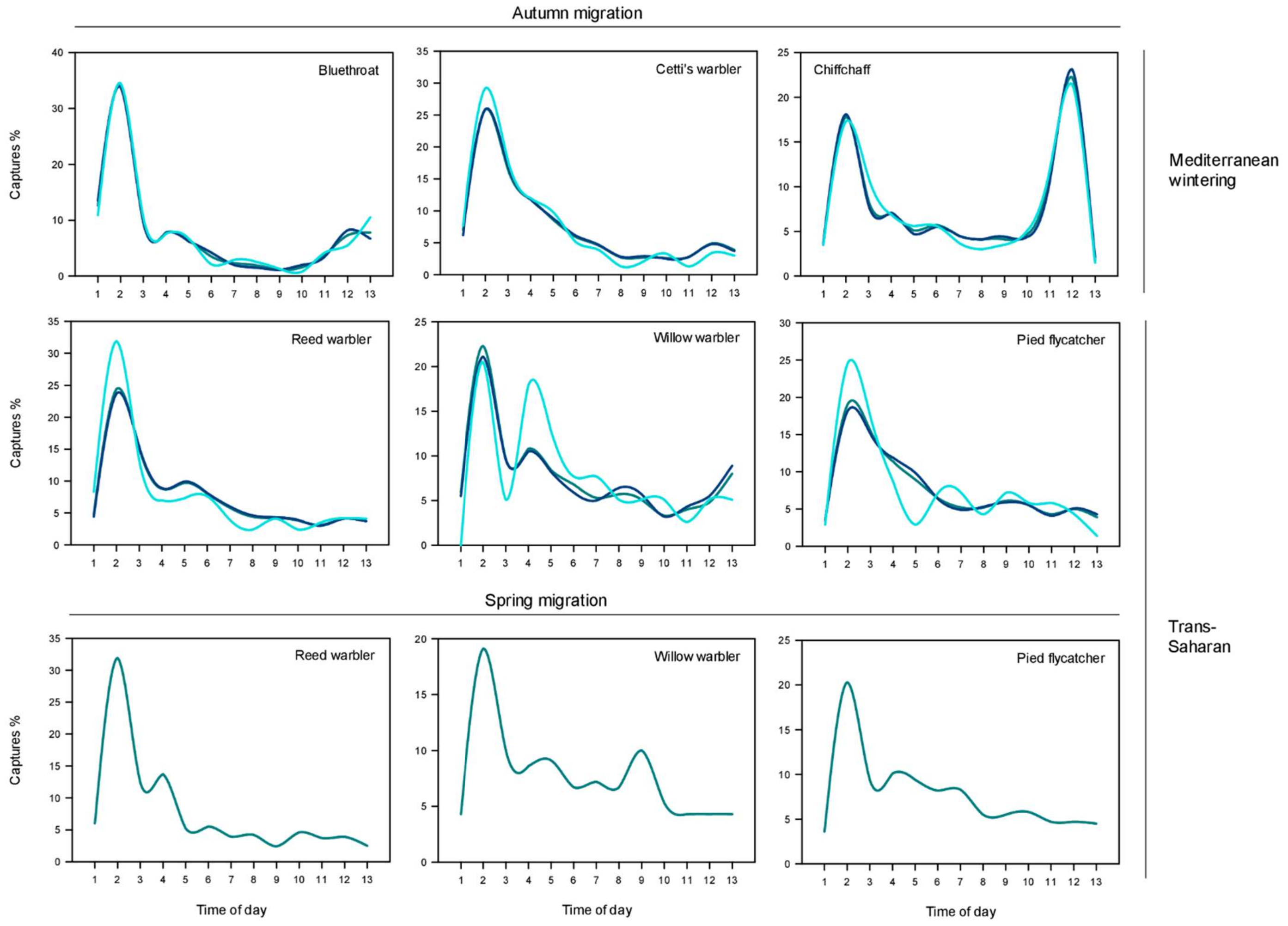

Figure 5.1. Diurnal activity, revealed by percentage of captures plotted against hours after sunrise (time of day), of total transients (green), adults (light blue) and first-year birds (dark blue) of Mediterranean wintering and trans-Saharan migrants during both migration seasons.

Estimates of diurnal body mass change

In autumn, both Mediterranean wintering and trans-Saharan transients gained weight during the day, except Pied flycatchers which were lighter late in the afternoon (Figure 5.2). Long distance migrants showed similar individual diurnal patterns for both seasons. After controlling for size, time of day was an important source of variation in the body mass response for all species during autumn and for Reed warblers during spring (Tables 5.2, 5.3 and 5.4).

Except for Bluethroats, age was another factor affecting body mass but only in Mediterranean wintering migrants: adults were in general heavier than juveniles. Diurnal variation of weight was similar for both age groups and for all species of both migration status, except for Reed warblers (Table 5.3) with an increase in body mass substantially stronger in adults than in first year birds (Figure 5.2).

The body condition of birds contributed importantly for the variation of body mass of transients of all studied species and for both seasons (Tables 5.2, 5.3 and 5.4). Fat birds were heavier than lean birds, as expected, showing that fat contributes significantly to body mass variation. The variation of body condition with time of day was significant for Chiffchaffs (Table 5.2) with lean birds gaining weight during the day while fat ones maintaining it instead (Figure 5.3).

Finally, post-breeding transients stopping over at different stages of migration showed different body mass among them for all species (Table 5.2 and 5.3). In general, late migrants were heavier than birds migrating early or during the main migration period, except for Bluethroats and Pied flycatchers. For the first species birds from the bulk of migration were heavier than early and late migrants, respectively. For Pied flycatchers, early birds considerably lost weight during the day while late birds increased it, however, the regression model didn’t fit for the data of these two subgroups, so the results may not be accurate (Table 5.5). Main migrants lost weight progressively from the first hour of daylight (Figure 5.4).

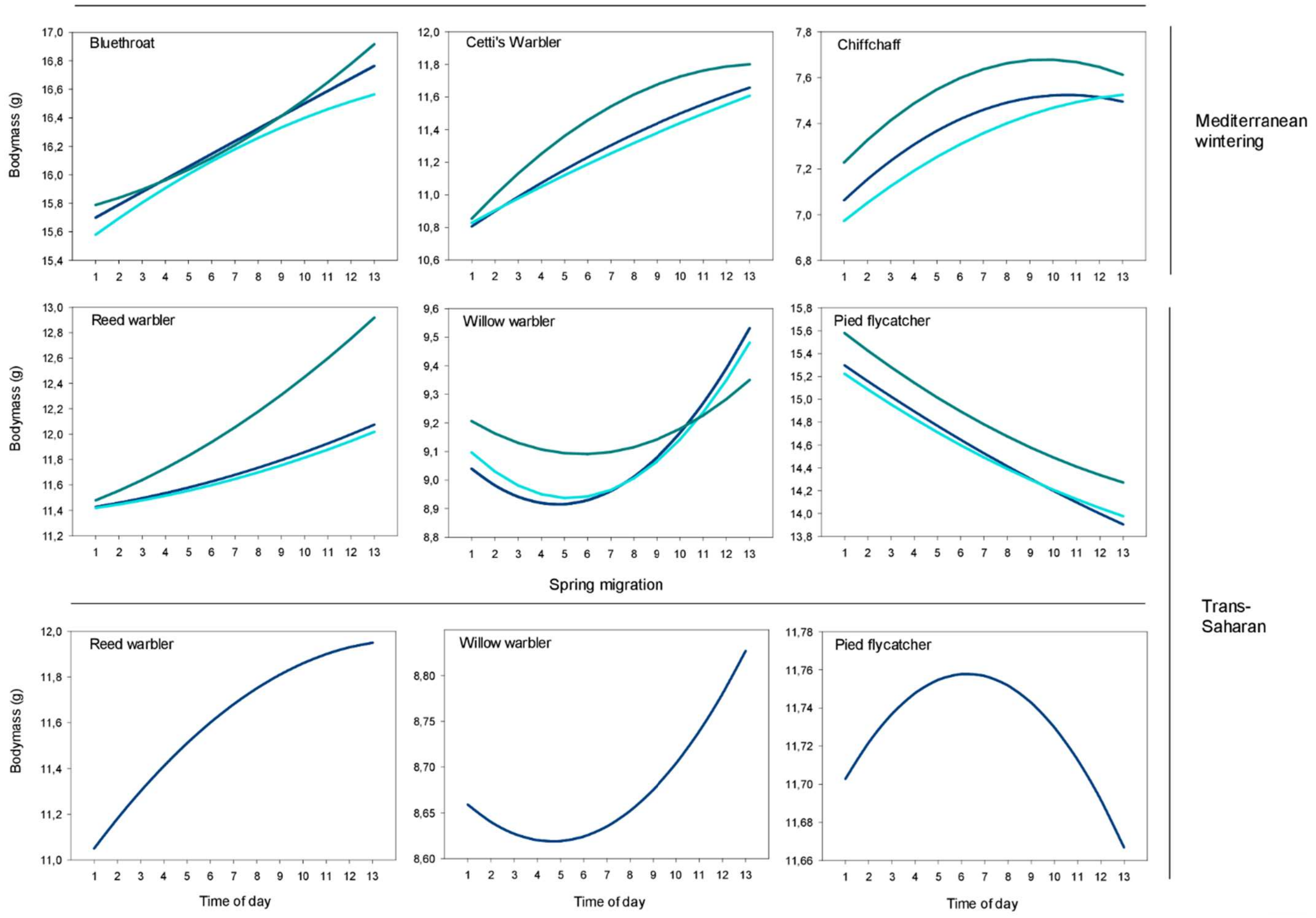

Figure 5.2. Estimated diurnal body mass changes of transients at Canal Vell (dark blue – total data set, light blue – first year birds and green – adults) during both seasons' stopovers based on a regression model with body mass as dependent variable, time of day (hours after sunrise), its square and length of primary 8 as independent variables.

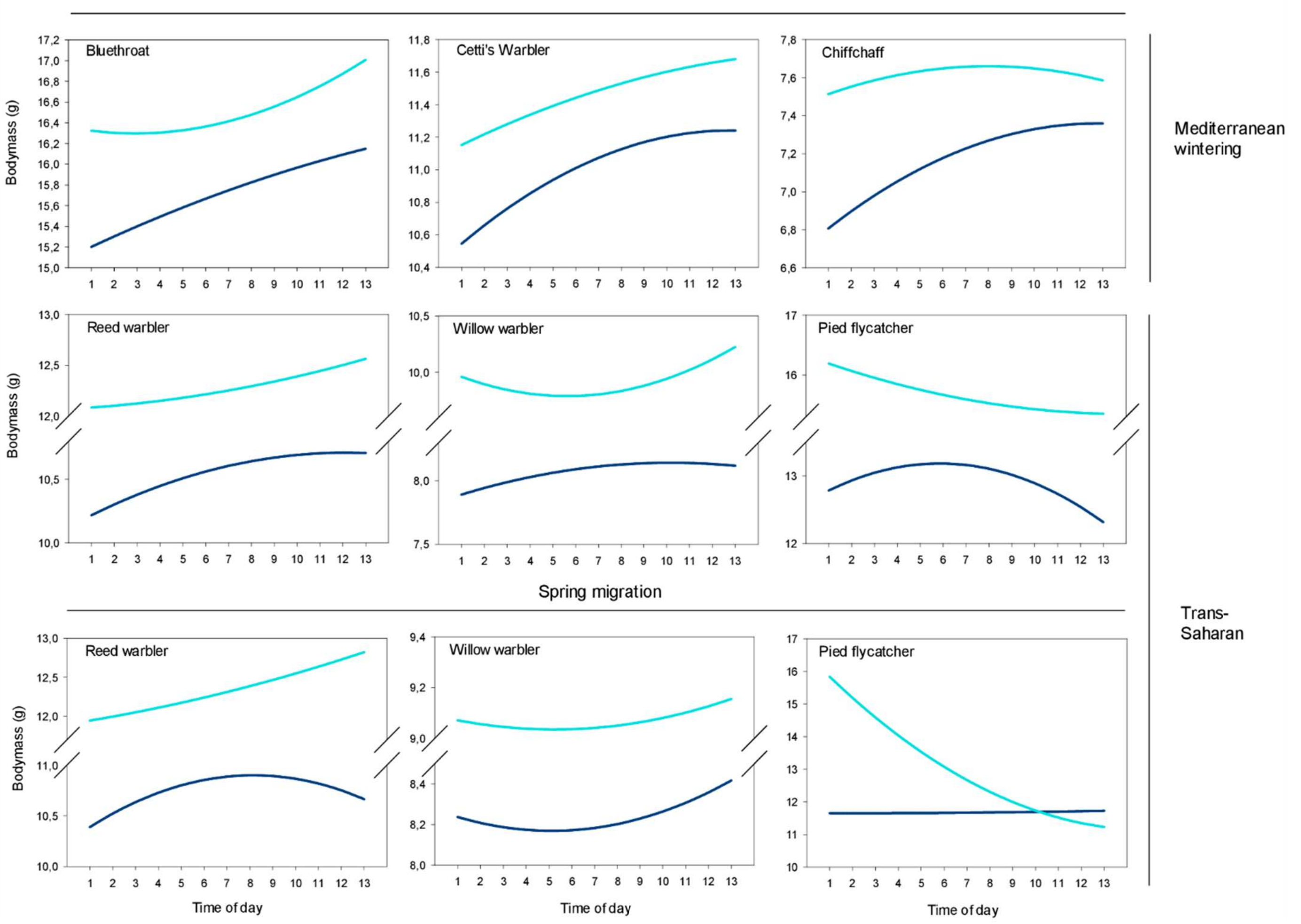

Figure 5.3. Estimated diurnal body mass changes of fat and lean transients at Canal Vell (dark blue – lean birds; light blue – fat birds) during both seasons' stopovers based on a regression model with body mass as dependent variable, time of day (hours after sunrise), its square and length of primary 8 as independent variables.

Table 5.2. ANCOVA analysis for body mass of Mediterranean wintering migrants during autumn in response to the factors age, body condition and migration stage, and the covariants primary length and time. df: degrees of freedom.

	Bluethroat				Cetti's warbler				Chiffchaff			
Source of variation	Type I sum of squares	df	F-value	Sig.	Type I sum of squares	df	F-value	Sig.	Type I sum of squares	df	F-value	Sig.
Corrected Model	458.08	11	28.58	**0.000**	4864.67	11	799.26	**0.000**	1527.67	11	518.58	**0.000**
Intersection	197942.52	1	135830.19	**0.000**	740467.09	1	1338231.78	**0.000**	401696.88	1	1499943.99	**0.000**
Primary length	204.42	1	140.28	**0.000**	4277.20	1	7730.10	**0.000**	922.88	1	3446.04	**0.000**
Time	100.93	1	69.26	**0.000**	280.24	1	506.48	**0.000**	196.53	1	733.86	**0.000**
Time^2	0.03	1	0.02	0.886	2.52	1	4.55	**0.033**	12.27	1	45.82	**0.000**
Age	0.25	1	0.17	0.680	12.68	1	22.91	**0.000**	5.46	1	20.38	**0.000**
Age*Time	0.11	1	0.08	0.779	1.72	1	3.11	0.078	0.79	1	2.97	0.085
Body condition	133.88	1	91.87	**0.000**	244.44	1	441.77	**0.000**	365.67	1	1365.43	**0.000**
Body condition*Time	2.69	1	1.84	0.175	1.96	1	3.55	0.060	19.66	1	73.43	**0.000**
Migration Stage	14.8	2	5.08	**0.006**	42.46	2	38.37	**0.000**	1.67	2	3.11	**0.045**
Migration Stage*Time	0.97	2	0.33	0.717	1.45	2	1.31	0.270	2.73	2	5.09	**0.006**
Error	1107.53	760			3308.84	5980			1968.12	7349		
Total	199508.13	772			748640.59	5992			405192.67	7361		
Corrected Total	1565.61	771			8173.50	5991			3495.79	7360		
Adjusted R^2	0.282				0.594				0.436			

Table 5.3. ANCOVA analysis for body mass of trans-Saharan migrants during autumn in response to the factors age, body condition and migration stage, and the covariants primary length and time. df: degrees of freedom.

	Reed warbler				Willow warbler				Pied flycatcher			
Source of variation	Type I sum of squares	df	F-value	Sig.	Type I sum of squares	df	F-value	Sig.	Type I sum of squares	df	F-value	Sig.
Corrected Model	7966.20	11	442.08	**0.000**	597.79	11	45.94	**0.000**	1189.14	11	52.49	**0.000**
Intersection	997637.89	1	608998.34	**0.000**	39172.77	1	33114.81	**0.000**	120523.88	1	58517.24	**0.000**
Primary length	2561.11	1	1563.40	**0.000**	203.01	1	171.61	**0.000**	74.95	1	36.39	**0.000**
Time	263.74	1	161.00	**0.000**	8.42	1	7.12	**0.008**	86.79	1	42.14	**0.000**
Time^2	4.35	1	2.65	0.103	6.03	1	5.09	**0.024**	0.48	1	0.23	0.630
Age	0.11	1	0.07	0.795	2.31	1	1.96	0.163	1.37	1	0.67	0.415
Age*Time	24.59	1	15.01	**0.000**	0.18	1	0.15	0.700	0.03	1	0.01	0.904
Body condition	4941.90	1	3016.73	**0.000**	356.02	1	300.96	**0.000**	1002.91	1	486.94	**0.000**
Body condition*Time	1.34	1	0.82	0.367	0.00	1	0.00	0.952	2.38	1	1.16	0.283
Migration Stage	166.77	2	50.90	**0.000**	19.59	2	8.28	**0.000**	14.89	2	3.62	**0.028**
Migration Stage*Time	2.30	2	0.70	0.496	2.23	2	0.94	0.391	5.34	2	1.30	0.275
Error	12083.08	7376			545.33	461			1122.50	545		
Total	1017687.17	7388			40315.89	473			122835.52	557		
Corrected Total	20049.28	7387			1143.12	472			2311.64	556		
Adjusted R^2	0.396				0.594				0.505			

Table 5.4. ANCOVA analysis for body mass of trans-Saharan migrants during spring in response to the factors age, body condition and migration stage, and the covariants primary length and time. df: degrees of freedom.

	Reed warbler				Willow warbler				Pied flycatcher			
Source of variation	Type I sum of squares	df	F-value	Sig.	Type I sum of squares	df	F-value	Sig.	Type I sum of squares	df	F-value	Sig.
Corrected Model	567.95	7	111.62	**0.000**	265.28	7	67.63	**0.000**	39.37	7	5.12	**0.000**
Intersection	87664.72	1	120597.70	**0.000**	56844.09	1	101446.03	**0.000**	28702.90	1	26149.14	**0.000**
Primary length	315.51	1	434.03	**0.000**	140.16	1	250.14	**0.000**	12.94	1	11.79	**0.001**
Time	46.81	1	64.40	**0.000**	1.05	1	1.88	0.171	0.00	1	0.00	0.947
Time^2	1.81	1	2.49	0.115	0.77	1	1.38	0.240	0.08	1	0.08	0.783
Body condition	199.40	1	274.31	**0.000**	120.33	1	214.75	**0.000**	23.09	1	21.04	**0.000**
Body condition*Time	1.13	1	1.55	0.213	0.03	1	0.05	0.824	1.63	1	1.48	0.225
Migration Stage	3.28	1	4.52	**0.034**	1.85	1	3.31	0.069	0.20	1	0.18	0.669
Migration Stage*Time	0.00	1	0.01	0.940	1.07	1	1.92	0.167	1.42	1	1.29	0.257
Error	481.22	662			419.69	749			219.53	200		
Total	88713.89	670			57529.06	757			28961.80	208		
Corrected Total	1049.17	669			684.97	756			258.90	207		
Adjusted R^2	0.536				0.383				0.122			

Chiffchaffs were the only species which diurnal variation of body mass was significantly different among migration stages (Table 5.2). Early birds steadily increased weight during the day, while the others increased faster but stabilizing by the second part of the day (main migrants) or even diminished (late migrants) (Figure 5.4). During spring, migration stage (defined as pentade) influenced significantly body mass only for Reed Warblers (Table 5.4).

The linear regression model applied for autumn data provides a better fit than the intercept-only model (without independent variables) for all species and sub groups except for Pied flycatchers body condition and migration stage (only early and late birds) (Table 5.5). For spring data, the model was significant for all species but again for Pied flycatcher, it did not fit the data for body condition (Table 5.6).

Table 5.5. Summary of r^2, *F*-statistics and corresponding *P*-values for each regression model for diurnal body mass change estimated for autumn transients.

Species	Sample	*n*	r^2	*F*	*P*
Bluethroat	Total	778	0.193	61.51	**0.000**
	First year	536	0.184	40.08	**0.000**
	Adults	236	0.202	20.85	**0.000**
	Lean	359	0.260	41.61	**0.000**
	Fat	419	0.161	48.75	**0.000**
	Early	41	0.459	10.45	**0.000**
	Main	674	0.179	9.17	**0.000**
	Late	63	0.263	7.01	**0.000**
Cetti’s Warbler	Total	6663	0.561	2841.94	**0.000**
	First-year	5405	0.556	2254.58	**0.000**
	Adults	596	0.596	291.50	**0.000**
	Lean	3326	0.607	1709.71	**0.000**
	Fat	3325	0.539	1291.88	**0.000**
	Early	331	0.429	81.82	**0.000**
	Main	5562	0.562	2375.40	**0.000**
	Late	770	0.601	385.26	**0.000**
Chiffchaff	Total	9128	0.323	1452.54	**0.000**
	First-year	5191	0.323	826.04	**0.000**
	Adults	2170	0.256	249.00	**0.000**
	Lean	4494	0.452	1236.63	**0.000**
	Fat	4634	0.249	512.09	**0.000**
	Early	737	0.345	128.52	**0.000**
	Main	7456	0.309	1112.18	**0.000**
	Late	935	0.394	202.04	**0.000**
Reed Warbler	Total	7393	0.142	407.45	**0.000**
	First-year	6765	0.139	362.82	**0.000**
	Adults	624	0.166	41.03	**0.000**
	Lean	2515	0.140	136.48	**0.000**
	Fat	4878	0.080	141.80	**0.000**
	Early	569	0.273	70.82	**0.000**
	Main	5729	0.143	318.94	**0.000**
	Late	1095	0.052	19.83	**0.000**

Table 5.5. (continuation) Summary of r^2, F-statistics and corresponding P-values for each regression model for diurnal body mass change estimated for autumn transients.

Species	Sample	*n*	r^2	*F*	*P*
Willow Warbler	Total	543	0.166	35.72	**0.000**
	First-year	434	0.183	32.11	**0.000**
	Adults	39	0.317	5.43	**0.004**
	Lean	253	0.267	30.20	**0.000**
	Fat	290	0.211	25,46	**0.000**
	Early	57	0.224	5.09	**0.004**
	Main	438	0.141	23.81	**0.000**
	Late	48	0.333	7.33	**0.000**
Pied Flycatcher	Total	559	0.068	13.60	**0.000**
	First-year	488	0.060	4.46	**0.000**
	Adults	69	0.171	10.28	**0.007**
	Lean	201	0.039	5.39	0.051
	Fat	7	0.641	8.86	0.323
	Early	16	0.292	1.65	0.230
	Main	517	0.080	14.87	**0.000**
	Late	26	0.114	0.95	0.435

Table 5.6. Summary of r^2, F-statistics and corresponding P-values for each regression model for diurnal body mass change estimated for trans-Saharan migrants during spring.

Species	Sample	*n*	r^2	*F*	*P*
Reed Warbler	Total	670	0.347	118.00	**0.000**
	Lean	331	0.365	62.53	**0.000**
	Fat	339	0.228	33.06	**0.000**
Willow Warbler	Total	757	0.207	65.64	**0.000**
	Lean	337	0.140	18.06	**0.000**
	Fat	420	0.311	62.73	**0.000**
Pied Flycatcher	Total	208	0.050	3.60	**0.014**
	Lean	201	0.039	2.63	0.051
	Fat	7	0.641	1.78	0.323

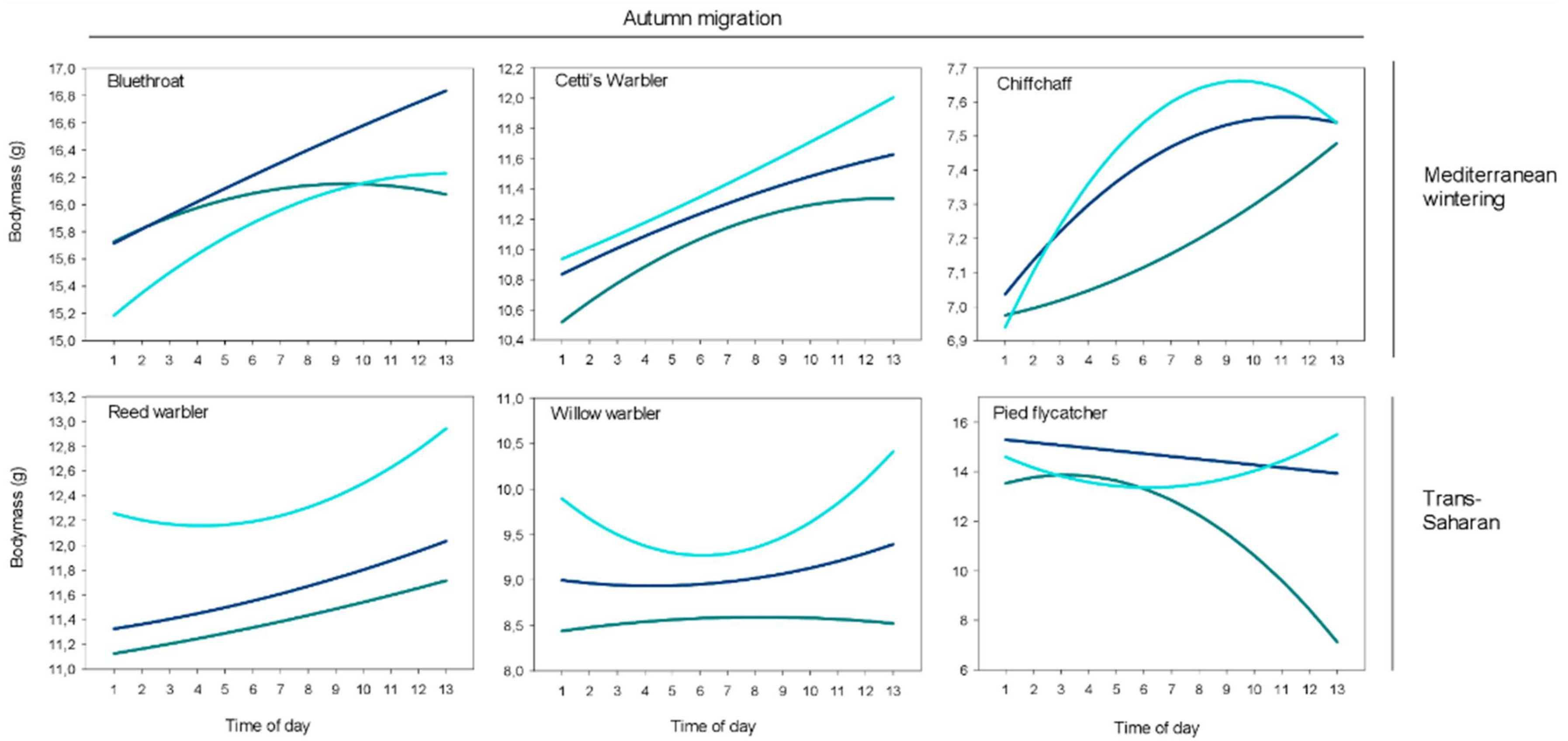

Figure 5.4. Estimation of diurnal body mass changes of transients in three different migration stages at Canal Vell (dark blue – main birds, green – early birds and light blue – late birds) during both seasons' stopovers based on a regression model with body mass as dependent variable, time of day (hours after sunrise), its square and length of primary 8 as independent variables

Diurnal fuel deposition rate (dFDR)

All species showed positive average dFDR during both migration seasons except Pied flycatchers, which was negative especially in autumn (Figure 5.5). Both in autumn as in spring average diurnal fat deposition rates were significantly different among species (autumn: $F_{(5,71)}$=63.7, p=0.000; spring: $F_{(2,35)}$=30.7, p=0.000)

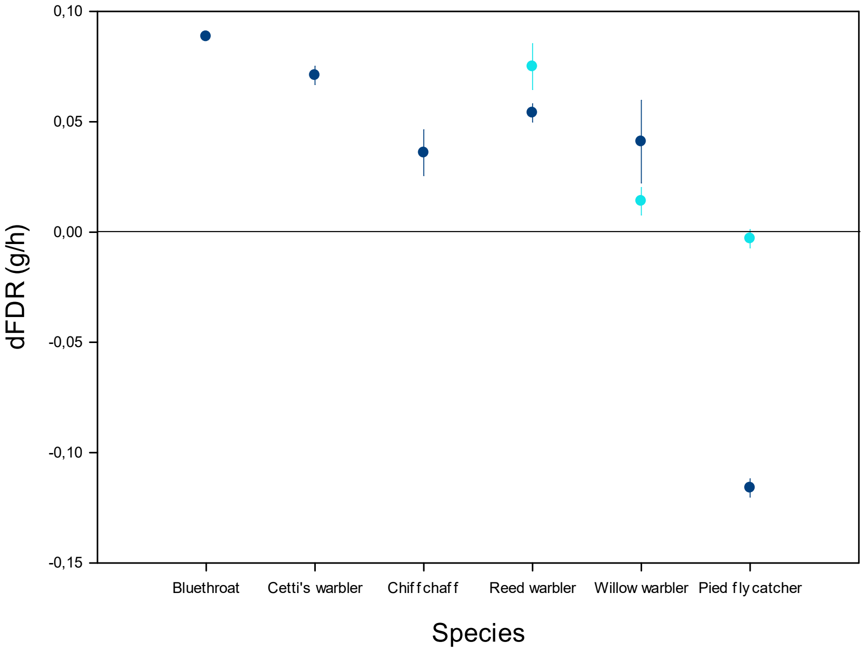

Figure 5.5. Mean ± SE diurnal fuel deposition rates for transients of Mediterranean wintering and trans-Saharan migrants during autumn (dark blue) and spring (light blue) stopover at Canal Vell.

Post-hoc tests showed that in autumn, Cetti's warblers, Chiffchaffs, Reed warblers and Willow warblers show similar positive dFDR, and this late species was related also with Bluethroats. There was no clear difference between dFDR of short and long-distance migrants. Pied flycatchers differed from all other species in autumn but its dFDR was similar to Willow warblers in spring because both dFDRs were close to zero.

During autumn and within the Mediterranean Wintering migrants, no statistic differences were found between age groups (Table 5.7). On the other hand, adult trans-Saharan Reed warblers showed significantly higher dFDR than first-year birds. For Chiffchaffs in autumn and Reed warblers and Pied flycatchers in spring, transients with different body conditions showed different dFDR. Lean birds showed higher diurnal refuelling rates for Chiffchaffs and Pied flycatchers, but fat Reed warblers refuelled faster (Figure 5.6). Pied flycatchers also showed differences among migration stages and dFDR increased notably with the progress of season, changing from a negative rate in early transients to a, near to zero, slightly positive one. Early Bluethroats showed also lower dFDR which increased substantially during the main migration period.

Table 5.7. Results for post-hoc Tamhane T2 test for pairwise comparisons. Similar pairs are highlighted (BT-Bluethroat, CW-Cetti's warbler, CC-Chiffchaff, RW-Reed warbler, WW-Willow warbler, PF-Pied flycatcher).

	(I) species	(J) species	Mean difference (I-J)	SE	Sig.
Autumn	**BT**	CW	0.0176	0.004	0.021
		CC	0.0526	0.010	0.006
		RW	0.0346	0.004	0.000
		WW	0.0476	0.019	0.341
		PF	0.2046	0.004	0.000
	CW	BT	-0.0176	0.004	0.021
		CC	0.0350	0.011	0.104
		RW	0.0170	0.006	0.121
		WW	0.0300	0.019	0.903
		PF	0.187	0.006	0.000
	CC	BT	-0.0526	0.010	0.006
		CW	-0.0350	0.011	0.104
		RW	-0.0180	0.011	0.876
		WW	-0.0050	0.021	1.000
		PF	0.152	0.011	0.000
	RW	BT	-0.0346	0.004	0.000
		CW	-0.0170	0.006	0.121
		CC	0.0180	0.011	0.876
		WW	0.0130	0.019	1.000
		PF	0.17	0.006	0.000
	WW	**BT**	-0.0476	0.019	0.341
		CW	-0.0300	0.019	0.903
		CC	0.0050	0.021	1.000
		RW	-0.0130	0.019	1.000
		PF	0.157	0.019	0.000
	PF	BT	-0.2046	0.004	0.000
		CW	-0.187	0.006	0.000
		CC	-0.152	0.011	0.000
		RW	-0.17	0.006	0.000
		WW	-0.157	0.019	0.000
Spring	RW	WW	0.061	0.012	0.000
		PF	0.078	0.011	0.000
	WW	RW	-0.061	0.012	0.000
		PF	0.0170	0.008	0.102
	PF	RW	-0.078	0.011	0.000
		WW	-0.0170	0.008	0.102

Table 5.8. One-way analysis of variance (migration stage) and t-test for independent variables (age and body condition) of diurnal fuel deposition rates for Mediterranean wintering and trans-Saharan migrants during autumn and spring stopovers.

	Mediterranean wintering						Trans-Saharan					
Independent variables	Bluethroat		Cetti's Warbler		Chiffchaff		Reed Warbler		Willow Warbler		Pied Flycatcher	
Autumn	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Migration stage	10.155	**0.000**	2.741	0.079	0.11	0.892	0.185	0.832	0.385	0.683	9.623	**0.001**
	t	p-value	t	p-value	t	p-value	t	p-value	t	p-value	t	p-value
Age	-1.153	0.261	-1.106	0.281	1.003	0.331	-7.519	**0.000**	0.933	0.364	0.480	0.636
Body condition	1.452	0.171	1.249	0.232	3.843	**0.001**	0.107	0.916	-0.17	0.868	0.840	0.416
Spring							t	p-value	t	p-value	t	p-value
Body condition							-2.355	**0.037**	0.859	0.403	7.812	**0.000**

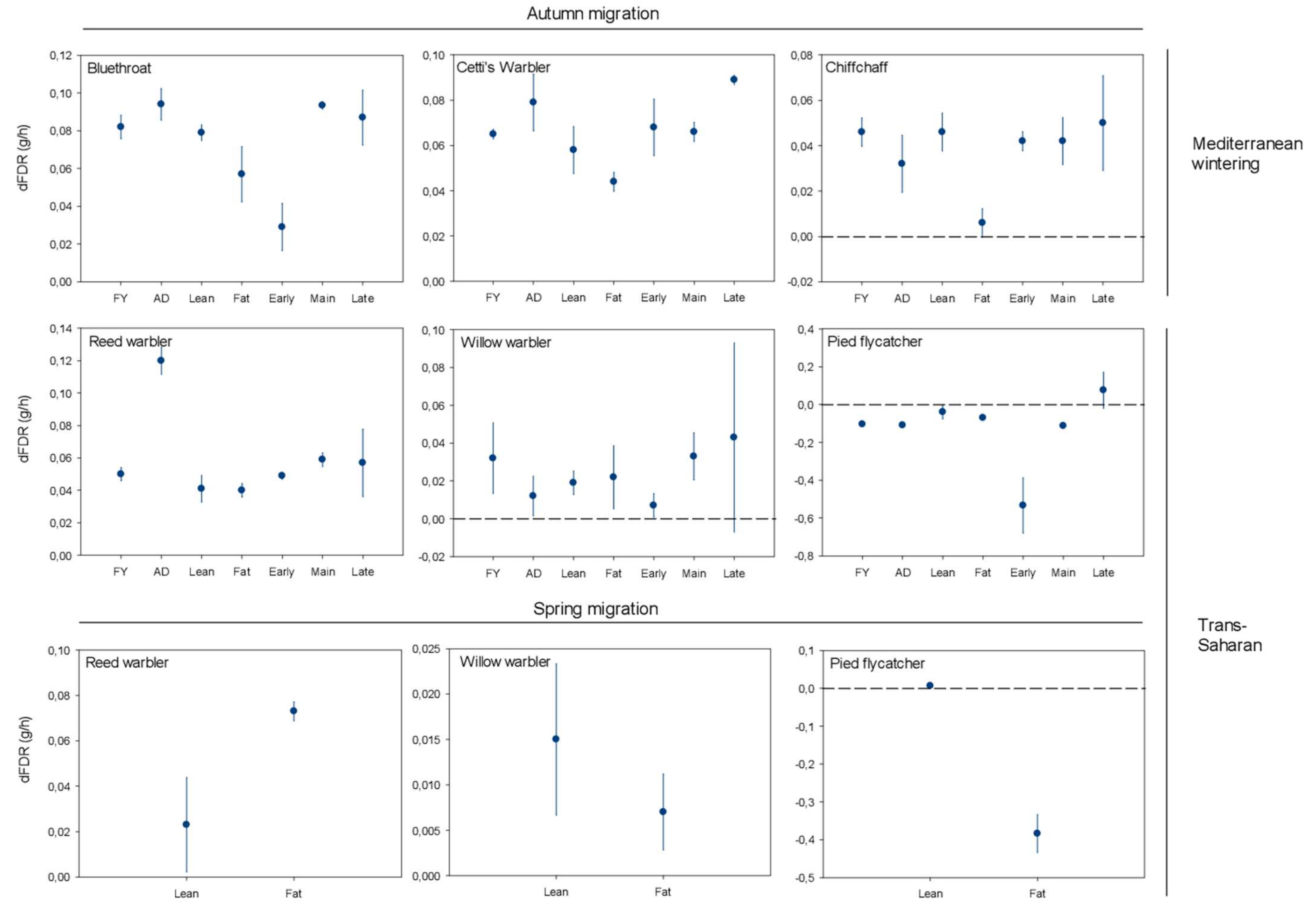

Figure 5.6. Diurnal fuel deposition rates (mean ± SE) of Mediterranean wintering migrants and trans-Saharan migrants during both seasons stopover at Canal Vell in relation to age (AD – adults, FY – first-year birds), body condition (lean and fat birds) and migration stage (early, main and late migrants)

Body mass at departure: late afternoon vs. dusk captures

In general, and for both autumn and spring migration, transients captured at dusk (i.e. during two hours after sunset) weighted less than those captured late in the afternoon (i.e. during two hours before sunset) (Figure 5.7).

The difference was significant during autumn stopovers for both Mediterranean wintering and trans-Saharan migrants except for Pied flycatchers. This difference could be due to fatload or to overall size of birds, but only for Bluethroats and Chiffchaffs differences in size were significant (Table 5.9). During spring migration birds captured at late afternoon and at dusk were of similar body mass and size.

Table 5.9. Mann-Whitney U test on body mass (weight) and size (f8) between late afternoon and dusk captures for each species and migration season.

		Autumn					Spring				
Species	Period	N	Body mass		Size		N	Body mass		Size	
			U	p-value	U	p-value		U	p-value	U	p-value
Bluethroat	late afternoon	119	5849.0	**0.026**	5895.0	**0.042**					
	dusk	118									
Cetti's warbler	late afternoon	594	65921.5	**0.000**	82135.0	0.225					
	dusk	292									
Chiffchaff	late afternoon	2191	49125.0	**0.000**	50604.5	**0.000**					
	dusk	63									
Reed warbler	late afternoon	584	158616.5	**0.006**	170936.5	0.607	627	631.0	0.078	765.0	0.621
	dusk	605					43				
Willow warbler	late afternoon	70	3505.5	**0.009**	4504.0	0.977	687	1964.0	0.752	1938.0	0.782
	dusk	129					70				
Pied flycatcher	late afternoon	50	1410.5	0.071	1725.0	0.938	190	86.0	0.128	86.5	0.129
	dusk	71					18				

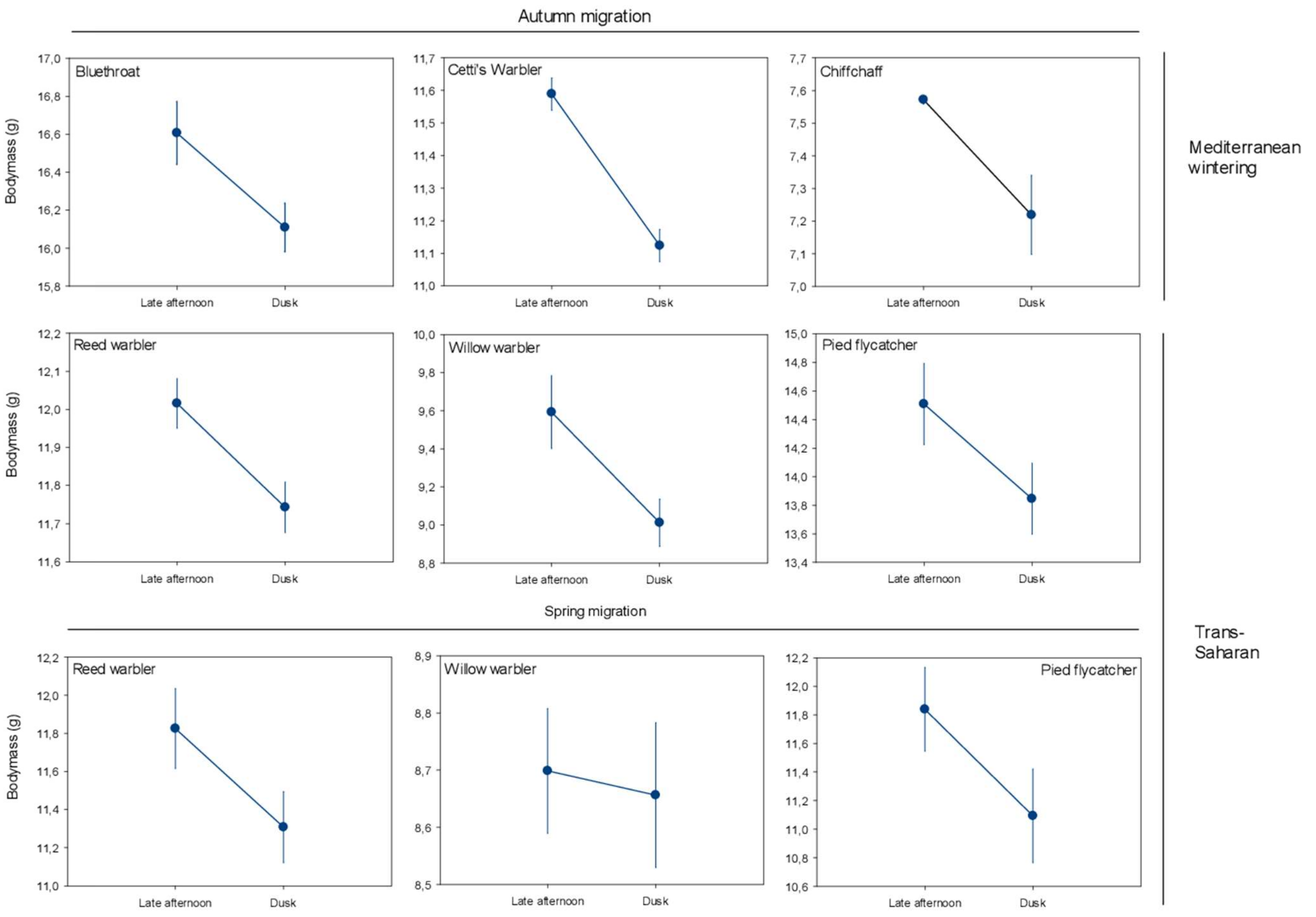

Figure 5.7. Mean ± SE body mass of Mediterranean wintering transients in autumn and trans-Saharan transients in autumn and spring captured during late afternoon and dusk

DISCUSSION

When and how active are transients on stopover?

Diurnal activity patterns can be related to body condition of birds because they reflect their foraging behaviour. During migration, many species switch from a double-peaked diurnal activity pattern to a single-peaked pattern in which the afternoon activity peak disappears (Brensing 1989). This change from the afternoon activity into migratory restlessness is dependent on fat deposition: only birds with fat reserves show distinct single-peaked activity patterns (Berthold 2001). More recently, Ramenofsky *et al.* (2003) stated that prior to migration, birds display two peaks of foraging. The first occurs in the early morning hours and the other around sunset. The pattern diverges once birds achieve migration season and enter in what they call the quiescent period – a transitional stage where certain birds cease feeding during evening twilight, display aphagia and roost. These birds migrate out of the area that same night after complete darkness. This period precedes onset of the night during spring and occurs in the early hours following onset of darkness during autumn.

At our site, transients of both migration status (short and long-distance migrants) were active mainly during the first hours in the morning during both migration seasons, as we would expect for birds on route. As we said before, at our site trans-Saharan migrants probably shifted the late peak into the night and change it to migratory activity, showing a quieter stage around sunset. Nevertheless, they were also active during the central hours of daylight in both seasons, but especially Willow warblers and Pied flycatchers during spring. For both species mean fat scores were similar or lower than in autumn migration (see Chapter 3) so their level of activity during the day may reflect the necessity to refuel or at least, maintain currently fuel loads before departure that same night. Or, that birds start migration earlier during the day, comparing with autumn because nights are shorter in spring (Sjöberg *et al.* 2017). In fact, just before the late period of almost inactivity and especially Willow warblers show an increase in captures that could be due to birds during migratory restlessness. The diurnal activity patterns of trans-Saharans were significantly different between seasons what may reflect the difference in the timing of both migration periods, as we know that spring passage occurs faster than in autumn (Tottrup *et al.* 2012, Nilsson *et al.* 2013).

Mediterranean wintering species (except Chiffchaffs), even with low average fat scores (Chapter 3) showed also a single-peaked pattern, although Bluethroats increased activity in late afternoon (Figure 5.1). The case of Cetti's Warblers, however, is different. With the lowest average fat score of all studied species (see Chapter 3) it revealed only a clear morning peak in its diurnal activity. Maybe a secondary afternoon peak would be expected, as this species regularly winters at our site, but if birds arriving at Canal Vell are still on the move or on dispersal, most of them will spread to other wintering areas in the Mediterranean region.

On the other hand, Chiffchaffs showed intense activity twice during daylight especially during late afternoon. Chiffchaffs are late migrants, arriving to Canal Vell only in October (Chapter 3), and show long stopovers combined with negative fuel deposition rates (Chapter 4), what could indicate that they are wintering and feeding during late afternoon, when overall temperature drops and there is more food available.

How does body mass change during daylight hours?

Regularly, fuel deposition rate (FDR) is defined as the average change in body mass per day, calculated as its difference between first capture and last recapture during the same migration season, and subsequently divided by the number of days between these two events. In the present study however, we analysed transient diurnal fuel deposition rate (dFDR), calculated from regression models of body mass with time of day. If transients are birds in good shape or with enough energy to continue migration, they only need to maintain their body condition and, therefore, dFDR would be positive or not less than zero. On the other hand, for birds that are refuelling, that is, that need to re-establish their optimal condition to go on with migration, dFDR should be high. Moreover, if our site is a suitable stopover area for refuelling, we should expect high fuel deposition rates at least for trans-Saharan migrants.

In this context, the positive trends of body mass estimations during the daylight hours (Figure 5.2) suggest that, in a general way, most migrants were gaining or maintaining their weight during the day at our site in autumn, except the Pied flycatcher that lost body mass considerably. In this case, the significant negative slope may predict that birds were either not feeding because of low food availability or were at a non-suitable or hostile stopover site for them (Alerstam and Lindström 1990, Ktitorov *et al.* 2008). We then may consider Canal Vell an acceptable stopover area for the rest of the species as they increased body mass during the day. However, the nocturnal losses of weight are unknown, and if they are higher than diurnal gains, it would lead to an overall daily loss of body mass, if birds decided to stopover more than one day. Winker *et al.* (1992) reported for an inland stopover site the case of some species showing positive diurnal gains that resulted in negative diel (24-h) gains upon subtraction of nocturnal losses. In Chapter 4 we saw that only Reed and Willow warblers refuelled at our site and the other species showed negative or null FDRs with rates rather lower than the mean rate estimated for passerines (Alerstam and Lindström 1990). This may be consequence of Canal Vell being a poor refuelling site or that birds use the area as a roosting site before the next flight episode. As discussed in Chapter 4, low to moderate mass gains at stopover sites in autumn might be expected for birds not approaching an ecological barrier (Winker 1995, Chudzińska *et al.* 2016), and migrants captured at our site are not facing such barrier but will certainly resume migration following the Mediterranean coast until the water body becomes narrower (Elgea and Arizaga 2016). Once birds have accumulated the energy reserves they need to continue migration, no further mass gain is required, and a good quality site is then a safe spot where mass can be maintained rather than gained (Dunn 2001). Therefore, we need to identify suitable "one-day" stopover areas, that is, suitable roosting areas for transients. These areas are not so good for refuelling birds in poor body condition, that need more time to recover from the previous flights, but nevertheless one-day areas must be essential for a successful migration. In this sense our study reveals that trans-Saharan migrants, like Willow warblers and Pied flycatchers on homeward migration, maintain their weight during the day probably because instead of feeding they just rest and resume migration in the following night. Moreover, we already know that stopovers for these species at Canal Vell last less than one day and most birds that use our site are transients (Chapter 4). On the other hand, Reed warblers which have an important breeding population at our site, slightly increased weight although less than one gram per day.

In alike investigations where diurnal body mass changes were estimated (Dunn, 2000; Winker *et al.*, 1992, Delingat *et al.* 2009) no significant negative slopes, like we found for the Pied flycatcher during both seasons, were reported. This situation is sometimes associated to problems inherent in small samples or slopes that are close to zero (Winker 1995) but in our case, at least the number of captures was relatively high, and the regression models fitted the data (see Table 5.5), although is true that this species showed negative mean dFDR, as we will see later.

Independently of birds losing or gaining weight, diurnal body mass evolved basically in three different ways (Figure 5.2):

(a) in a linear pattern, constantly throughout the day, increasing or decreasing (Bluethroats, Cetti's warblers, Pied flycatcher in autumn),

(b) in an asymptotic pattern, increasing during the day and stabilizing late in the afternoon (Chiffchaffs, Reed warblers in spring), and

(c) in a non-linear U shape pattern, decreasing in the beginning of the day but increasing towards late afternoon (Willow warblers).

A linear or close to linear mass gain, like our (a) and (b) patterns was found already by Dunn (2000) for Magnolia warblers *Dendroica magnolia* during fall migration in Long Point, Ontario. However, in the same study but during spring, birds did not gain much mass until several hours after sunrise but then increased weight significantly towards the end of the day, in what somehow resembles our (c) pattern, although at our site body mass decreases after dawn. The (a) and (b) patterns were expected, as transients spend part of the day foraging and increasing their mass towards the night when they resume migration. The (c) pattern, however, occurs when birds lose weight after their arrival at the stopover site and then must spend the central hours of the day foraging to recover, as we saw reflected in the diurnal activity patterns of Willow warblers during spring (Figure 5.1).

The use of recaptures to calculate fuel deposition rates revealed negative or very low refuelling for most birds at Canal Vell (Chapter 4), but in this study we found that dFDR rates were, in general, positive. Winker *et al.* (1992) already questioned whether the mass changes of recaptures should be considered indicative of general migrant populations and that daily changes in mass tend to be greater in magnitude among entire transient populations than among the minority of individuals recaptured. Nevertheless, here we did not take in account nocturnal losses, so eventually overall fuel deposition rates would be finally negative or very low, according with the results exposed in Chapter 4.

The energetic component of stopover is influenced by environmental factors like interspecific competition (see Jenni and Schaub 2003). In our site, adult Reed warblers. increased weight considerably faster than juveniles (Figure 5.2) and their dFDR was higher (Figure 5.6). This may indicate that adults are more experienced when searching for food or for a good foraging area. The fact that subordinate and less experienced birds were expected to have lower FDR than adults was analysed also in Chapter 4, but we concluded then that age only shaped overall FDR for Bluethroats.

Endogenous factors like energy stores at arrival and time programme, i.e. progress of season, were also evaluated after we found in the previous chapter that refuelling relied in part upon these factors. Body condition played an important role on diurnal body mass dynamics. Fat birds of all species were heavier than lean ones what validates that fat contributes to the overall weight of birds. Moreover, lean Chiffchaffs in autumn and Pied flycatchers in spring showed higher dFDR than fat birds (Figure 5.6). This behaviour was described for birds after crossing an ecological barrier (Loria and Moore 1990, Kuenzi *et al.* 1991), what would be the case of Pied flycatchers with lean birds maintaining weight while fat birds showed negative dFDR. Chiffchaffs' behaviour in autumn cannot be explained by the same arguments, though. Lean and fat birds gained weight with different patterns and fat individuals maintained their body mass while juveniles increased weight towards the end of the day (Table 5.2, Figure 5.3). This is supported by our findings that dFDR is higher for lean Chiffchaffs (Figure 5.6) as we would expect from a species which winters in our area and does not have to cross ecological barriers, when refuelling must be higher in fat birds (Schaub and Jenni 2001). For the other trans-Saharans in autumn, body condition was not a determinant factor when shaping diurnal body mass changes, and fat and lean birds gained weight with similar patterns. During spring, although, fat Reed warblers had higher dFDR than lean birds, and were birds probably preparing for the breeding season.

During outward migration, it is known that the progress of season accelerates migratory fuel deposition (Fransson 1998, Dänhart and Lindström 2001) and that late migrating individuals have higher fuel stores, higher FDR and seem to travel at higher speed (e.g. Ellegren 1993, Fransson 1995, Schaub and Jenni 2000a, b). This means that body condition varies among early, main and late transients independently of their species (Chapter 4) and our results support this statement (Tables 5.2 and 5.3). For all but two species, late birds were heavier (Figure 5.4) although in a significant way only for Pied flycatchers (Table 5.8, Figure 5.6). Furthermore, late birds showed positive dFDR forced by the time pressure to finish migration. Late in the season, there is no time to waste searching for a better stopover area and birds may try to cross the Mediterranean directly or stopping over in some Balearic island, as we already proposed in Chapter 4.

In the case of Bluethroats, heavier birds with higher dFDR passed during their main migration period. Late birds were lighter as if they were ending migration and did not need to refuel so intensely.

In spring, although the annual study period was short, the time programme was responsible for body mass changes in Reed warblers (Table 5.4). This species has an important breeding population in the Ebro delta that could have influenced the results, although it is impossible to know how within this study. In the analysis performed in Chapter 4 these differences were not found.

Now we know that independently of their average body mass, transients put weight similarly during the day, whatever the stage of migration they are (Figure 5.4). Only Chiffchaffs showed some differences in this matter and early birds increased weight constantly till late afternoon, while late birds did it more intensely in the first half of the daylight period.

Tonight we fly.

If transients leave the stopover site immediately after sunset or in the following hours to reengage migration (Bruderer 1997, Schmaljohan *et al.* 2013, Müller *et al*. 2016), we could think that due to migratory restlessness birds captured at dusk (i.e. after sunset) are the ones preparing for leave. Alternatively, birds captured late in the afternoon (i.e. before sunset) would be individuals staying more days in the area, taking advantage of this period for foraging as food availability (mainly insects) at this hour of the day is high. In either case, we could think that some parameters like body mass (as a proxy of body condition) and size (if birds are from different ages or populations) may differ between individuals captured at dusk or the hour before.

In this context, during autumn migration and for all species, birds captured at dusk were lighter. This may indicate that, at least for trans-Saharan migrants, these are not the birds that restart migration but that are feeding and probably stopping over that night. For Mediterranean wintering species instead, it could be birds that have reached their winter quarters or are already near. In the case of Reed and Willow warblers we know that lean birds make longer stopovers than fat ones (Chapter 4). Moreover, the number of trans-Saharan migrants captured at dusk is higher than in the late afternoon (Table 5.9). We could think that these are long distance transients starting migratory restlessness and preparing to depart, after passing the quiescent period (Ramenofsky *et al*. 2003). But as we saw before, after sunset birds are lighter, thence two things may occur: a) birds in better body condition start leaving the stopover before sunset and birds with low fat deposits start later at night or b) birds captured at dusk are not showing migratory restlessness but are foraging instead of departing.

The mean body mass of Mediterranean wintering species also differed between birds active at dusk or at late afternoon when more birds were captured. Knowing that especially Bluethroats and Chiffchaffs winter at our site, probably there is a combination of individuals already wintering and birds that are still on migration. Like Reed and Willow warblers, lean Chiffchaffs had longer stopovers (Chapter 4), but in this case birds are lighter because they are also smaller (Table 5.9), so it is impossible to know if the difference between individuals captured at dusk and during late afternoon is due to body condition or size. For Bluethroats, on the contrary, birds captured at dusk were lighter but bigger than birds active during late afternoon, and probably were birds foraging as they start wintering or will resume migration after stopover to refuel at our site. This could be related to what was stated in Chapter 4 where adult Bluethroats longer stopovers were influenced by dominant and most experienced birds established already on their winter quarters and forcing juveniles to continue their search for other suitable wintering areas.

Final remarks

At Canal Vell the main activity period for transients was the first 4 hours of daylight, as already described for birds on stopover. Trans-Saharan migrants show a quieter stage around sunset and probably shift the late peak into the night as they become restlessness. Trans-Saharans show different activity patterns between spring and autumn. The migration period in spring is always shorter than in autumn and this may affect how birds use the stopover site.

Willow warblers and Pied flycatchers during spring, with low mean fat scores, were also active at midday to ensure the preservation of currently fuel loads before departure that same night. But because of time constraints during the pre-breeding migration they may also resume migration earlier in the day.

Bluethroats and Cetti's warblers showed also a single-peaked pattern, although Bluethroats increased activity in late afternoon. As wintering species at our site, a secondary afternoon peak would be expected for Cetti's warblers unless birds are still on migration or dispersal. Only Chiffchaffs showed a two-peak activity pattern with its maximum during late afternoon. These could be foraging wintering birds.

Positive trends of body mass estimations suggest that, in a general way, migrants were gaining or maintaining weight during the day at our site in autumn. Canal Vell is an acceptable stopover area if nocturnal losses are not higher than diurnal gains or if birds are transients. Low fuel deposition rates are reflecting a poor refuelling site and birds choose to roost before resume migration following the Mediterranean coast.

If transients are majority in some stopover sites it is important to identify suitable "one-day" stopover areas. Areas were transients can roost safely and even forage enough to maintain their body condition. Although they are not so good for refuelling, these areas are essential for a successful migration and the conservation of migrant songbirds.

Two interesting patterns come out from the diurnal body mass change estimations. Pied flycatcher showed a negative slope for diurnal mass change during both seasons, not found in other similar studies where birds always increased body mass somehow. Willow warblers body mass evolved in a non-linear U-shape pattern, with a loss of weight in the middle of the day and a strong increase towards late afternoon, preparing for departure.

In previous chapters we found that most species had a negative or very low daily refuelling rate but, in this study, dFDR rates were in general, positive. However, after accounting nocturnal body mass losses, the overall daily fuel deposition rate may well be at the end, negative or very low.

Age conditioned diurnal body mass changes in Reed warblers with adults increasing weight faster than juveniles, as they are more experienced foraging. In Chapter 4 we found that intraspecific competition only shaped overall FDR for Bluethroats.

Body condition contributed to the overall weight of birds. For all species, fat birds were heavier than lean birds. These lighter lean birds, in some species, showed higher dFDR, a behaviour reported for birds after crossing an ecological barrier as could be the case of Pied flycatcher in spring but is also common when birds are not facing a long flight, like Chiffchaffs in autumn or Reed warblers in spring. For trans-Saharan species in autumn, however, body condition was not a determinant factor when shaping diurnal body mass patterns, and fat and lean birds gain weight during the day similarly.

The progress of season accelerates migratory fuel deposition at least for Pied flycatchers during autumn migration. Late migrants were significantly heavier and showed higher dFDR than earlier birds as they were time pressed and needed to refuel faster. This significant increase in the refuelling rate of late birds can come from the lack of time to keep flying and stopping over along the coast and the possibility that they try to cross the Mediterranean directly from the Ebro delta, with a probable stopover in some Balearic island, as proposed already in Chapter 4. In a short distance migrant like the Bluethroat, late birds were lighter and probably were birds already wintering or close to their wintering quarters. In fact, maximum refuelling rates for this species occur during the main period of migration.

In spring, the time programme affected body mass of Reed Warblers as they are already close to their breeding quarters, while the other trans-Saharan species still need several days to reach theirs. Nevertheless, we did not find these differences in the previous chapter of this thesis. Independently of their average body mass, and except Chiffchaffs, transients put weight similarly throughout the day, whatever the stage of migration they were.

For all species in autumn, birds captured after sunset were lighter than birds captured before and were probably birds foraging while stopping over more than one day. Long distance migrants in better body condition may be inactive in that period of time preparing to resume migration later in the night. In the case of Reed and Willow warblers we know from Chapter 4 that lean birds make longer stopovers than fat ones. Moreover, the number of trans-Saharan migrants captured at dusk was higher than in late afternoon probably since birds in better body condition start leaving the stopover before sunset and birds with low fat deposits do it later at night or that birds captured at dusk are not showing migratory restlessness but are foraging instead of departing.

Mediterranean wintering species were more active during late afternoon. Bluethroats and Chiffchaffs winter at our site so the pattern is the result of a combination of some individuals already wintering and others that were still on migration. Chiffchaffs captured at dusk were lighter and, similarly to trans-Saharan species, lean birds stopover longer than fat ones (Chapter 4) although in this case these birds were in average smaller and it is impossible to know if weight differences are due to body condition or size. If different populations stopover at the Ebro delta these could be birds that have reached already their winter quarters.

In another way, Bluethroats captured at dusk were lighter but bigger but probably were wintering birds, as intraspecific competition could determine the selection of wintering grounds with smaller birds forced to resume migration. We relate this to what was stated in Chapter 4 where adult Bluethroats longer stopovers were influenced by dominant and most experienced birds established already on their winter quarters and forcing juveniles to continue their search for other suitable wintering areas.

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CHAPTER VI

This must be the place: habitat preferences of migrant songbirds during stopover in a coastal location.

INTRODUCTION

As we have been seeing in former chapters of this thesis, stopover sites are of great importance for birds migrating twice a year between breeding and nonbreeding grounds. In fact, songbirds often spend more time and energy at stopover sites (Hedenström and Alerstam 1997, Wikelski *et al*. 2003) than they spend flying. Refuelling efficiency during stopover will then directly influence a migrant's energetic condition and time schedule, which can carry-over to affect arrival timing, breeding or wintering territory quality, and ultimately overall fitness and survival of the bird (Aebischer *et al*. 1996, Dänhardt and Lindström 2001, Smith and Moore 2005, Harrison *et al*. 2011, MacDade et al. 2011). Habitat characteristics and food availability at a stopover site may be the principal determinants of refuelling rates (Schaub and Jenni 2001, Dunn 2002, Lindström 2003). Although habitat is a very important factor to achieve a successful migration, the majority of migrant songbirds, especially long-distance ones, must efficiently select on route the stopover sites from among unfamiliar habitats that vary in structure and food availability (Catry *et al*. 2004; Rodewald and Brittingham 2007). The search for a suitable habitat is even harder for nocturnal songbird migrants as they are time constraint because they cease flight mainly before dawn when visibility is limited, when only proximate cues are available for suitable landing and all of this is aggravated with a general lack of information (Bolshakov *et al*. 2003, Mukhin *et al*. 2008).

In this chapter we make a first approach to habitat preferences of Mediterranean wintering and trans-Saharan migrants during both migration periods at a stopover site near a coastal lagoon in the Ebro delta, where reedbeds are the dominant habitat but where some shrub patches are present. We will focus on transient birds (see Chapter 4) as they preponderate over birds that stay for refuelling. We compare specific body condition in both main microhabitats referred before, one dominated by reedbed and the other, a patchy shrub habitat. We also model habitat preference of songbirds in relation to several main factors as migration season, their status as short or long-distance migrants, the species and body condition at arrival. We expect that habitat preferences will be somehow related to variables that can be quantified and help to determine suitable stopover sites along the route. To know the habitat preferences of migrants in a particular stopover site will help also to improve the area by potentiating the most appropriate habitat or mosaic of habitats.

STUDY AREA AND METHODS

A total of 41 mist-nets were installed in the northern shore of the Canal Vell (40º44'N, 00º47'E), a coastal lagoon in the Ebro delta, dominated by large extensions of flooded reedbed, mostly of *Phragmites australis* and *Typha angustifolia*, with some shrub areas *Myoporum tenuifolium* and *Tamarix sp*. Birds were captured in two types of habitat, with different vegetation composition, defined as "reed" and "bush" habitats. We called "reed" to the habitat formed by an extensive mass of *Phragmites australis* with a line of *Arundo donax* along a path in the border of the reedbed and we called "bush" to two shrub areas, one with mostly *Myoporum tenuifolium* and the other dominated by shrubby *Tamarix sp.* plants (Figure 6.1).

Figure 6.1. Mist-nets location in the Canal Vell lagoon in both habitats, "reed" (orange polygons) and "bush" (green polygons).

Data were collected in a standardized way following the European-African Songbird Migration Network manual of field methods (Bairlein 1995) in both autumn (1992-2000) and spring (1996-2000) migration seasons (see Chapter 2 for description of study site).

Birds were ringed, aged and wing length was measured to the 0.5mm (see Svensson 1992, Jenni and Winkler 1994). Body mass was recorded to the nearest 0.1g using an electronic scale and the accumulated body fat was scored using a visual nine-level scale (Kaiser 1993). For each bird, time of capture to the nearest hour was registered.

Like in former chapters, we selected both short to medium- and long-distance migrant species. Bluethroat (*Luscinia svecica*), Cetti's warbler (*Cettia cetti*) and the Chiffchaff (*Phylloscopus collybita*) as Mediterranean wintering birds and Reed warbler (*Acrocephalus scirpaceus*), Willow warbler (*Phylloscopus trochilus*) and Pied flycatcher (*Ficedula hypoleuca*) as trans-Saharan migrants. Reed warblers captured before the 24 of august were set aside to exclude birds from local breeding populations (Cramp 1998, Schaub and Jenni 2000).

Statistical analyses

We only analysed transient birds, that is, birds captured once in the season as they represent is the major number of captures in our area (see Chapter 4). Birds were split in two groups following body condition. Birds with fat scores under the specific median were classified as lean and birds with fat scores equal or above the median, as fat birds. We corrected body mass values to 12:00h, because of diurnal weight variation (Chapter 5) to elude bias related to time of capture. Specific corrected body mass and fat score were compared between both habitat types using the t-test for independent samples, preceded by the Levene's test for equality of variances.

To analyse the effect of the covariates season (spring/autumn), status (trans-Saharan/Mediterranean wintering), species and body condition (lean/fat) on the dependent dichotomous variable habitat (reed/bush) we used a binary logistic regression. This is a predictive analysis, used to describe data and to explain the relationship between one dependent binary variable and one or more nominal, ordinal, interval or ratio-level independent variables. All statistical tests were performed with SPSS 24.0 package (SPSS Inc. 2016).

RESULTS

During autumn, captures in bush habitats were higher except for Reed warblers and Bluethroats, that preferred reed habitats. Mediterranean wintering species showed similar body mass in both habitat types, although not for fat scores. Except for Cetti's warblers with no statistical differences regarding none of the body measurements, birds captured on bush habitats were fatter than birds using reed habitats (Table 6.1, Bluethroat $t_{(866)}=2.448$, p=0.015, Chiffchaff $t_{(5858,518)}=2.433$, p=0.015). Long-distance Reed and Willow warblers showed significantly different mean body mass and fat scores depending on the habitat they were caught [corrected body mass (cbm): Reed warbler $t_{(7055,497)}=-4.959$, $p=0.000$, Willow warbler $t_{(536)}=1.994$, $p=0.047$; fat score: Reed warbler $t_{(7884)}=-6.480$, $p=0.000$, Willow warbler $t_{(663)}=3.630$, $p=0.000$]. Reed warblers captured on reed were heavier and fatter, on the contrary for Willow warbles with leaner and lighter birds captured in reed habitats. During spring no differences were found in body mass nor fat scores between habitats. In a general way, captures were higher in bush habitats, except for Bluethroats and Reed warblers, this last species only in autumn. In spring, Reed warblers' capture figures were matched in both habitats.

Table 6.1. Total number of captures, corrected body mass (cbm, mean±SE) and fat score (fs, mean±SE) for each habitat and species. Significant different means between habitats (significant t-test results) are highlighted.

Autumn	Bluethroat					Cetti's warbler					Chiffchaff				
	N	cbm	SE	fs	SE	N	cbm	SE	fs	SE	N	cbm	SE	fs	SE
Reed	568	16.19	0.07	**1.93**	**0.05**	2839	11.24	0.02	1.91	0.02	2950	7.39	0.01	**2.23**	**0.02**
Bush	301	16.11	0.08	**2.13**	**0.07**	4087	11.24	0.02	1.92	0.01	5614	7.39	0.01	**2.29**	**0.01**
Autumn	Reed warbler					Willow warbler					Pied flycatcher				
	N	cbm	SE	fs	SE	N	cbm	SE	fs	SE	N	cbm	SE	fs	SE
Reed	4260	**11.77**	**0.03**	**3.22**	**0.03**	210	**8.68**	**0.11**	**2.90**	**0.12**	144	14.34	0.18	3.60	0.12
Bush	3627	**11.58**	**0.03**	**3.03**	**0.02**	455	**8.97**	**0.08**	**3.39**	**0.07**	483	14.67	0.10	3.63	0.05
Spring	Reed warbler					Willow warbler					Pied flycatcher				
	N	cbm	SE	fs	SE	N	cbm	SE	fs	SE	N	cbm	SE	fs	SE
Reed	298	11.52	0.07	2.95	0.07	121	8.53	0.08	3.29	0.07	26	11.46	0.22	1.76	0.19
Bush	305	11.46	0.08	2.93	0.06	642	8.59	0.04	3.33	0.03	182	11.75	0.09	2.01	0.09

Binary logistic regression indicated that season, status and species were significant predictors of habitat preferences [Table 6.2, Chi-Square=381.388, df=4 and *p*=0.000 (<0.05)]. The predictor body condition was not significant. All the four predictors "explained" only 1.9% of the variability of habitat preferences (Nagelkerke R^2=0.019). Season, status and species were significant at the 5% level (Table 6.2). The odds ratio (OR) for season was 1.723 (95% CI 1.531 – 1.940), for status was 1.963 (95% CI 1.809 – 2.131) and for species the corresponding figures were 0.795 (95% CI: 0.772 – 0.819). The model gave an overall percentage correct prediction rate of 60.2%.

Table 6.2. Estimates of the Binary Logistic Regression of 27085 ringed birds for habitat type and four predictors: season (Autumn/Spring), status (trans-Saharan/Mediterranean winering), species and body condition (fa/lean).

Predictors	B	SE	Wald	Gl	Sig.	Exp(B)
Season	0.544	0.060	81.078	1	**0.000**	1.723
Status	0.675	0.042	260.166	1	**0.000**	1.963
Species	-0.230	0.015	231.500	1	**0.000**	0.795
Body condition	0.036	0.025	2.085	1	0.149	1.037
Constant	-5.371	2.518	4.549	1	**0.033**	0.005

DISCUSSION

Different migrants assess stopover sites with similar mechanisms along their migratory routes and these common attributes may be widely applied to identify stopover locations of conservation importance for migratory species (McCabe and Olsen 2015). If we could identify the factors that influence habitat preferences during stopover we can use it to select similar locations susceptible of being officially protected.

As a matter of fact, our results reveal that some variables may predict part of the habitat preferences of transient birds at our area. One of these predictors was migration season. During spring, for instance, all species showed similar weight and fat scores in both habitats and were captured mainly in bush habitats, although for Reed warblers' captures were even. Spring migration takes place at our site in more or less a month and birds have less time to choose the more favourable habitat or to spend it in stopover (Chapter 4; Tottrup *et al.* 2012, Nilsson *et al.* 2013), for that reason any habitat that ensures proper food availability and shelter to maintain or slightly improve body condition while waiting for the next flight probably in the same day of arrival, may be good enough (Dunn 2001).

In other way, autumn is a much more protracted migration season and most species showed higher capture numbers also in bush habitats, but Reed warblers and Bluethroats were captured mainly in reed habitats, certainly due to food preferences and feeding habits (del Hoyo *et al*. 2005, 2006). In fact, species as well as migration status (in the end, groups of species) were also a predictor of habitat preference (Table 6.2). Mediterranean wintering species weight similar in both habitat types, but except for Cetti's, warblers, birds were fatter on bush habitats (Table 6.1). Two out of three long-distance migrants showed habitat differences concerning body features. Reed warblers were heavier and fatter on reed habitats, what would be expected since they are well adapted to this type of environment and correlation exists between habitat and morphology for this species (Leisler *et al*. 1989). Moreover, dominant birds may choose first the most favourable habitat when they arrive to the site after the previous migratory flight. The same occurred for Willow warblers in bush habitats where birds were also heavier and fatter. Evidence of strongly habitat-related body mass was already found for European Robins *Erithacus rubecula* in the Eastern Baltic and birds captured in two different habitats (hardwood and coastal scrub) showed different body mass of (Chernetsov 2013). Four out of six species of both migration status (Chiffchaff, Cetti's Warbler, Willow warbler and Pied flycatcher) preferred shrubby habitats since captures were higher there. Bluethroats and Reed warblers instead, were present in major number in reed habitats as we said before.

Body condition did not predict habitat preference and we cannot correlate the level of fat accumulation with the habitat transients are using at least at our site. However, the predictors of the model explained less than 2% of the variability of habitat preferences. Other intrinsic and extrinsic factors may be involved when choosing of stopover habitat is involved. For instance, Woodworth *et al*. (2014) found that although coastal stopover sites may be important during songbird migration, mortality can be higher and habitat poorer than in more inland sites. Birds then, as an adaptive strategy for individuals that initially settle at the coast, may relocate in more inland sites to rest and refuel before they continue migration.

Final remarks.

Habitat preferences of transient birds at our area can be predicted in some extent by factors like season, migration status and species. During spring, body condition was not important for habitat preferences and birds were captured mainly in bushes, even Reed warblers, although the number of captures of this species in both habitats were similar.

In autumn most species also preferred bushes except Reed warblers and Bluethroats that were captured mainly in reed habitats. Most of the Mediterranean wintering species were fatter on bush habitats. Also, most of the long-distance migrants showed habitat differences concerning body condition. Reed warblers were heavier and fatter in reed and Willow warblers in bush habitats. Almost all species preferred habitats dominated by bushes and this is reflected in the number of captures in this habitat. Only Bluethroats and Reed warblers were caught mainly in the reedbed.

Although for some species body condition showed some variation between habitats when we use it to model habitat preference this factor was not significant. However, the predictors did not explain much variability in the model, since other intrinsic or extrinsic factors may be involved.

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CHAPTER VII

General discussion and conclusions

Migration is a dangerous endeavour but unavoidable for survival and migrant songbirds have high odds not to make it. Every year more than 2 billion breeding songbirds in Europe (Hahn *et al*. 2009) cross mountains, sea and desert, twice, to attain their wintering quarters in Africa and get back. In the best of the cases, some species will winter in the Mediterranean Basin. Their journey consists basically on the alternance of nocturnal flight and diurnal rest. These daily rests can become longer stopovers if birds need to restore energy spent previously or if they are near an ecological barrier. Therefore, suitable stopover areas along the route, i.e. areas where food is available and predation risk is low, are essential for the conservation of migrant songbird populations.

In the Palaearctic-African migration system, the coastal Mediterranean areas provide important stopover sites as birds tend to migrate along the coast trying to reach the point of crossover in the southern Iberian Peninsula. The Ebro delta is located along this route and its wetlands are frequented regularly by songbirds during both migration seasons. In fact, standardized bird ringing campaigns are performed each year since 1992, in spring and autumn, to monitor migratory songbirds and collect environmental and biometrical data. Such amount of data can be used to explore stopover behaviour of both trans-Saharan and Mediterranean wintering migrants that stopover in the Ebro delta. Some of the species breed here, some winter here and some stopover while preparing for the next flight bout. Because of these different exploitations of the area it is an appropriate place to investigate stopover ecology of songbirds with different migratory behaviours during their entire life-cycle.

Therefore, compelled by my commitment with the land that welcomed me almost 25 years ago, and by the evidence that depending on how attractive or colourful is the studied subject more attention and consideration it will have, I decided, instead, to focus my work in a group of generally unnoticed birds, more or less all brown or greenish, but abundant in the Ebro delta where they breed, winter and migrate throughout European priority conservation habitats like coastal lagoons. I used bird ringing data to investigate about stopover ecology and although I’m not a bird ringer (yet. It is my new objective after this thesis, hope I get it in less than 20 years) I helped in ringing campaigns and entering the data that I analysed in the aftermath. Also, I would like to claim the importance of standardized ringing procedures that we have all over Europe as well as a great number of ringing stations where thousands of birds are ringed every year. This generate an amount of data that we should not obviate. It is true that actually there are other methods a lot more precise that can allow us to investigate migrant birds, even at the individual level, but they still are a minority and should be used to analyse further on and complement the basic research that we can do using ringing data. In the same way ringing data can help to interpret the results of the new techniques to study bird migration. Moreover, if we think about conservation and the importance of environmental education to create awareness between citizens of our fragile world, bird ringing can be a very useful tool. In the case of songbirds, to observe these little birds in hand and so close, after explaining their migratory feats, lead people to understand the importance of conserving suitable places where they can rest and restore energies.

With this in mind, in this thesis I drew the outlines of stopover ecology in the Ebro delta, a wetland of international value, and with the information gathered I aim to contribute to future conservation plans which can be extrapolate for similar coastal wetlands and must consider the ecological needs of migratory songbird populations. I explored the main subjects of stopover ecology, such as temporality of passage, body condition, length of stopover, fuel deposition rates and habitat preferences, for six passerine species that stopover at our site. I chose these species, first for its number of captures and second for its general migratory behaviour as I was looking to get the whole picture of what was happening during stopover in both migration seasons. Half of them were long-distance trans-Saharan migrants (Reed and Willow warblers and Pied flycatchers) and the other half were short to medium-distance Mediterranean wintering species (Bluethroats, Cetti’s warblers and Chiffchaffs). If total time of migration depends mainly on stopover decisions and these decisions depend on when birds perform migration (Chapter 3), where they stopover (Chapter 6), their physical condition and how it changes during stopover (Chapter 4 and 5), I expected Mediterranean wintering and trans-Saharan migrants to behave differently between them and between seasons in relation to the intrinsic and extrinsic factors that may shape stopover ecology. Each chapter of the thesis has its own detailed discussion so here I’ll examine the cardinal findings of my work.

As I started with the question “when?” I saw that migration patterns of long- and short to medium-distance migrants were different in both seasons what helps to avoid temporal cohabitation of similar species and so elude competition for food resources and habitat niche. Similar species show greater time gap between time of appearance at our site (the case of Willow warblers and Chiffchaffs). In more detail, during autumn, long distance migrants migrated earlier due to a constraint phenology pattern (Chapter 3) and an average higher speed of migration (Ellegren 1993). They also carried more fat especially late birds maximizing speed and prioritising overall time of migration (Alerstam and Lindström 1990). Short to medium-distance migrants were leaner near the end of migration as expected for birds near winter quarters with less travel to do and these results are supported by the GLM model where we tested body mass response to factors like age and covariates like wing and their interaction with time.

During pre-breeding migration, when long-distance migrants arrived to the stopover site, Mediterranean wintering birds were no longer there, what is consistent with very low capture numbers obtained for this group. We also detected the evidence of loop migrations of Willow warblers and Pied flycatchers, both species with higher capture figures during spring than during autumn.

Weight and fat accumulation showed some relationship as heavier birds were in most cases the fatter ones, but for some species other factors may be also involved. One of these factors was size of birds measured by its wing length, that I decided to include in our GLM model for size control purposes and to have more reliable outputs. I found the evidence of age differences for some species that supported previous results like adult trans-Saharan birds start migration before juveniles and vice versa for some Mediterranean wintering species (Berthold 2001). It is worth noting that I describe, for the first time, age differences relative to phenology patterns for Chiffchaffs. Also, that our area is a catch-up area for Willow warblers and Bluethroats with both age groups migrating simultaneously and no evidence of the differences reported for stopover sites located before and after the Ebro delta (see Ellegren 1990, Lindström *et al.* 1996, Correia 2013).

After analysing when and in what physical condition birds used our site, I decided to investigate for how long did they stay and also what energetic body changes were observed during the stopover by analysing fuel deposition rates (FDR) (Chapter 4).

First of all, estimated real stopover durations were shorter than expected (e.g. Schaub *et al*. 2001) due to the presence of transients, i. e. birds that stop over for only one or two days. Additionally, the fact that the Ebro delta is a wintering area for some of the species helped to inflate estimations of minimum stopover durations.

During autumn, Mediterranean wintering species stayed longer at the site, more than five days, and the time was increasing towards the end of migration. They had null or negative FDR what may indicate they were near the end of migration. Trans Saharan birds instead, showed shorter stopovers (between 2 and 4 days) and low initial FDR, that increased towards the end of the season as expected in time minimization migration strategies, supported by the fact that lean long-distance birds refuelled faster. These results were sustained by the general linear model I used to test the effect on FDR of different parameters like migration status and body mass. In addition, late birds stayed longer and refuelled faster so I propose that birds change from an assumed hop strategy (few short leaps) (Elgea and Arizaga 2016) to longer jumps along the coast or eventually try to cross the Mediterranean in a direct flight or using the Balearic islands as bridge between both continents. During spring, trans-Saharan migrants stopped over for less time than in autumn, without refuelling nor losing weight neither, what suits a well-known faster homeward migration behaviour.

The models tested did not permit to relate FDR with stopover duration and for that reason other extrinsic or intrinsic factors may be involved shaping the time component of stopover. Age for instance, can be one of these factors. Longer stopovers were observed for juvenile long-distance migrants as well as for adult short to medium-distance migrants. An interesting fact derived from stopover analysis was that Chiffchaffs behaved like long-distance migrants in what I think is the result of the existence of different subspecies of different breeding origins that come together in the Ebro delta (Perez-Tris *et al*. 2003).

In Chapter 5 I investigated diurnal stopover behaviour of transients, using birds captured only once. Outside migration periods, songbirds are active mainly in the morning and late in the afternoon. During stopover instead, all species were active mostly in the first hours of daylight as expected for birds still en route. Trans-Saharans shifted afternoon peak to night restlessness with a quieter period just before. Nevertheless, long distance migrants showed some amount of activity also in the central hours of the day, especially in spring, probably to maintain fat deposits or refuel before leaving the site in the same night. This result is supported, for instance, by diurnal FDR (dFDR) patterns we found for Willow warblers. On the other hand, most Mediterranean wintering species were also active in late afternoon, especially Chifchaffs. These birds were probably already wintering and may take advantage of the increase in food availability when temperatures go down. However, Cetti's warblers, also wintering in the Ebro delta, lacked this late peak what could indicate that some dispersion is still going on.

I used a regression model of body mass with time of day to estimate dFDR. In general, all species got heavier during the day and only Pied flycatchers lost weight what is new if compared with other similar studies (e.g. Dunn 2000). Nevertheless, during autumn although mean dFDR was negative, late birds indeed refuelled what supports the theory that this species may try the direct flight to Africa. Regarding departure from the stopover site, birds were in general lighter after sunset what may indicate that those birds were foraging and would stay at least another day. Heavy birds probably left the area before or around sunset. Nevertheless, these results must be taken with caution because what I called dFDR reflects body mass changes during the day and these changes do not necessarily mean fuel deposition. In the case of birds captured later in the day it could be due to stomach filling, for example.

Finally, if I pretended to know how to identify suitable stopover areas susceptible of protection, I had to explore habitat preferences (in our case microhabitats dominated by reed or bushes) among both trans-Saharan and Mediterranean wintering migrants. I used a binary logistic regression to model habitat preferences and it revealed that season, migratory status and species were factors that predicted which kind of habitat birds were in to. During spring for instance, all migrants showed high capture rates in bushes, even Reed warblers, but body condition was similar between habitats. In fact, body condition was not a predictor although we must be careful because of the low percentage of variability the model explained and so other intrinsic or extrinsic factors were for sure involved. During autumn most of the species preferred bushes and they were in general fatter there. Reed warblers and Bluethroats preferred the reed habitat instead, as they are better adapted to forage in this habitat.

The Ebro delta performance as a stopover site in the Palaearctic-African migration system.

Songbirds stopover in the Ebro delta differently depending on season. During outward migration lean long-distance migrants showed higher fuel deposition rates and at the same time fat birds had shorter stopovers what could suggest birds were facing a typical refuelling site. Nevertheless, stopovers were in general shorter than expected what could indicate that, even if some refuelling was possible, birds were moving along the coast in several short hops without the need of intense fat deposition and the Ebro delta was not the last stopover before crossing the Mediterranean Sea.

In spring, instead, the area is located eventually after a barrier for trans-Saharan migrants, as I derive from Pied flycatchers and Willow warblers' number of captures, stopover length, body mass variations and fuel deposition rates. Birds maintain weight and leave soon, optimizing time and energy. The Ebro delta can be a valuable resting site for long distance migrants in their homeward migration and it is included in the route of already known loop migrations.

Something in common for both seasons were short stopovers of long-distance migrants. In this thesis I put forward that the Ebro delta is a good quality site for transients maximizing speed of migration as they need to make one-day stopovers to rest between consecutive flight bouts. Even without heavy refuelling, these short stops are essential for the overall success of migration and eventually for the survival of trans-Saharan migrants. The Ebro delta is then, a roosting site where birds rest and wait for the next flight and where fuel deposition is low. These low values are consistent and were obtained with different estimation methods.

From stopover length and fuel deposition rate patterns obtained in this thesis I could infer that the Ebro delta is not a staging refuelling site and low refuelling rates may indicate low food availability. As found in other studies, the area should have more woody habitat cover to improve refuelling rates (Ktitorov *et al*. 2008). The best stopover habitat should be then a mosaic of different vegetation structures where bush patches, reedbeds and also trees should dwell. By the time the data were collected the reedbed predominated over other kind of habitats and having only large extensions of reed habitat could be disadvantageous for species not well adapted in terms of foraging habits, and then ultimately, they tend to relocate to more suitable areas. These areas may be situated inland but I think that birds first search for better places in the different habitats of the Ebro delta and to understand these movements further studies would be necessary and different sites within the delta should be compared.

I also propose the enlargement in time of spring ringing campaigns to include Mediterranean wintering migrants as their passage occurs before trans-Saharans and with the actual timing we are losing information about this group of migrants. Nevertheless, short to medium-distance migrants can at the long last, adapt better to habitat changes has they have more time to search for the best place to winter.

Finally, the data I used was collected 20 years ago, and a lot of variation happened in Canal Vell area until now. During these last years, hydrological dynamics of this coastal lagoon changed, salinity levels are higher now and the inputs of fresh water were reduced. This fact caused some changes in vegetation with the reduction of reedbed areas (Figure 7.1). I then propose that new analyses should be carried out with more recent data to explore possible changes in the migrant songbird community stopping over in the area.

Figure 7.1. The Canal Vell ringing site in the year 2000 (left) and 2018 (right). Note reedbed reduction due to the general increase in water salinity levels these last years.

Conclusions

1. First of all, ringing data are an easily available resource to conduct migration research due to actual huge data sets stored and should be used more often. At the same time bird-ringing campaigns can be used to increase environmental awareness among people.

2. Trans-Saharan and Mediterranean wintering birds show in general different phenology patterns, avoiding as much as possible the overlap between similar species using the area at the same time. Also, body condition is different between late birds of the two groups. Late long-distance migrants carry more fat than short to medium-distance migrants at the same time, revealing different migration strategies due to time and energy constraints. There is also the evidence of loop migrations in spring performed by Willow warblers and Pied flycatchers. Age differences relative to phenology patterns are described for the first time in Chiffchaffs and the Ebro delta is a catch-up area for both age groups of Willow warblers and Bluethroats.

3. Estimated real stopover durations were shorter than expected and the presence of transients was high. Mediterranean wintering species stayed longer in the site than trans-Saharan migrants. The study of fuel deposition rates supports the hypothesis of the time minimization-based theories for long-distance migrants. During autumn, time pressed late trans-Saharan migrants may change from the usual hop strategy along the coast to perform longer jumps following the same route or eventually cross the Mediterranean through the Balearic Islands. Chiffchaffs behaved like long-distance migrants regarding some stopover parameters as the result of the existence of different subspecies with different breeding origins that use the area while en route. Estimated fuel deposition rates were low or inexistent for almost all species.

4. All species were more active during the first morning hours. Long-distance migrants were somehow active also during the central hours of the day probably because of foraging to maintain actual fat deposits that will permit them to resume migration that same day. Mediterranean wintering species were active

also in late afternoon, especially Chiffchaffs with some birds probably already wintering in the area. The only species that lost weight during the daylight hours were Pied flycatchers although late birds increased diurnal fat deposition rate supporting the theory of the direct flight to Africa. In general, diurnal fuel deposition rates were low but positive although nocturnal losses were not computed, and overall fuel deposition rate may be low or negative. Heavy transients left the area near sunset and birds captured after dusk were probably foraging and stayed in the area at least one more day.

5. Differences in habitat use were found between seasons. In spring birds were captured mainly in bushes but body condition was similar in both habitats (reed and bush habitats). During autumn most species preferred bush habitat and were fatter there except Reed warblers and Bluethroats captured mainly in reed habitats where they are better adapted.

6. The Ebro delta is not the last stopover area before Mediterranean crossing in autumn but is the first area located after the cross of this barrier in spring for some long-distance species that perform loop migrations. During both seasons the Ebro delta is a suitable one-day stopover area for transients, and even with low refuelling rates is essential for overall success of songbird migration.

7. The best stopover habitat would include the alternation of different habitats like reedbeds, bush patches and even trees. If reedbeds predominate, species not well adapted in terms of foraging habits, for instance, may relocate in other areas, in the same delta or inland. Further studies on these movements should be carried out.

8. If the understanding of migration behaviour of Mediterranean wintering species is desired, the spring ringing time should be enlarged to include these birds. Actually, they leave the area before ringing efforts start.

9. Finally, as data here analysed was collected almost 20 years ago it would be interesting to analyse more recent available data to explore possible changes in the migrant songbird community due to habitat variation observed as a result of hydrological changes in the lagoon.

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