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DEPARTAMENTO DE CIÊNCIAS DA VIDA

FACULDADE DE CIÊNCIAS E TECNOLOGIA
UNIVERSIDADE DE COIMBRA

To be or not to be a specialist: feeding and refuelling by reed warblers in Portugal

André F. C. Silveira

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Coimbra para cumprimento dos requisitos
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André Filipe da Conceição Silveira

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Abstract

Reed beds are associations of hydrophyte vegetation that includes species of different families. They are also the natural habitat of specialized fauna such as migratory passerines who make stopovers during their migration between Europe and sub-Saharan Africa. This study assesses the quality of two reed beds in Central Portugal, Paul do Taipal and Paul da Madriz, for two insectivore passerine species, *Acrocephalus scirpaceus* (Reed Warbler) and *Acrocephalus schoenobaenus* (Sedge Warbler), similar in physiology but with contrasting migratory strategies and feeding habits.

Ringing data from 12 years was used to evaluate habitat use for both study species and to determine productivity of breeding Reed Warblers. Environmental factors were used to explain stopover duration and body weight variation during spring and autumn migration. The birds' body condition was assessed and compared between species, seasons and age. Blood samples were taken to assess triglycerides and glucose blood levels, which are considered to distinguish migratory strategies. Abundance of food items present in the environment was determined by counting arthropods in the field to determine possible differences in stopover quality, with emphasis on the Sedge Warbler's preferred food, *Hyalopteris prunis* aphids. Finally, bird faeces were collected and examined to assess bird diet and preference in both reed beds.

This study shows that Paul do Taipal was used more extensively than Paul da Madriz for both species. North Atlantic Oscillation and Northern Annular Mode values between December and March were the environmental parameters more correlated with stopover duration for both migratory seasons, whereas precipitation in North Africa and wind speed in Portugal were the most important parameters to explain body weight

variation in spring and autumn migration, respectively. The body condition of Reed and Sedge Warblers were both greater during the autumn migration than during the spring migration. Productivity of Reed Warbler has been increasing in Paul do Taipal, despite the reduction in adults and juveniles. Triglycerides values differed between species and glucose between seasons with concentrations higher in Sedge Warblers and the autumn migration, respectively. Arthropod abundance varied for almost all orders between months, with higher numbers in summer. As expected, the peak of abundance of aphids coincided with the peak of passage by Sedge Warblers, but the relationship between the two variables was not significant. Food items most consumed by both passerines in both reed beds were Coleoptera and Hymenoptera. According to Ivlev Indices, there was a preference for Coleoptera and Hymenoptera in Paul do Taipal for both species and a preference for Coleoptera, Hymenoptera, Hemiptera and Diptera in Paul da Madriz for Reed Warblers.

These results show that Paul do Taipal seems to be a better stopover site due to increased abundance and diversity of food items and use by both Sedge and Reed Warblers. Environmental parameters are very important in determining the stopover duration of these two passerines. Metabolite blood levels are in accordance with Reed Warbler making stopovers in Portugal before and after crossing the Mediterranean, while Sedge Warblers do not seem to fatten up in Portuguese reed beds.

Keywords: Palearctic passerines, reed beds, migratory strategies, stopover

Resumo

Caniçais são associações de plantas hidrófitas que incluem espécies de várias famílias. São também o habitat natural de fauna especializada, tal como passeriformes migradores que fazem paragens durante a sua migração entre a Europa e a África subsariana. Este estudo avalia a qualidade de dois caniçais no centro de Portugal, Paul do Taipal e Paul da Madriz, para duas espécies de passeriformes migradores, *Acrocephalus scirpaceus* (Rouxinol-pequeno-dos-caniços) e *Acrocephalus schoenobaenus* (Felosa-dos-juncos), semelhantes fisiologicamente mas com estratégias migratórias e hábitos alimentares contrastantes.

Doze anos de dados de anilhagem científica foram usados para avaliar o uso de habitat para ambas as espécies de estudo e determinar a produtividade de Rouxinóis reprodutores. Fatores ambientais foram usados para explicar a duração de paragens e variação de peso durante a migração primaveril e outonal. A condição corporal dos pássaros foi determinada e comparada entre espécies, épocas e idades. Amostras de sangue foram recolhidas para avaliar níveis de triglicéridos e glucose no sangue, que se consideram poder distinguir estratégias migratórias. A abundância de itens alimentares presentes no ambiente foi determinada através de contagens de artrópodes no campo para determinar possíveis diferenças na qualidade das paragens, com ênfase na comida preferida da Felosa, afídeos *Hyalopterus prunis*. Finalmente, foram recolhidas fezes das espécies de estudo e examinadas para determinar a dieta e preferência das aves em ambos os caniçais.

Este estudo mostra que o Paul do Taipal foi usado mais extensivamente do que o Paul da Madriz por ambas as espécies. Os parâmetros mais correlacionados com a duração de paragem para ambas as épocas de migração foram os valores da North

Atlantic Oscillation e Northern Annular Mode entre Dezembro e Março, enquanto a precipitação no Norte de África e a velocidade do vento em Portugal foram os parâmetros mais importantes para explicar a variação de peso na migração primaveril e outonal, respectivamente. A condição corporal dos Rouxinóis e das Felosas foram maiores durante a migração outonal do que durante a migração primaveril. A produtividade dos Rouxinóis tem vindo a aumentar no Paul do Taipal, apesar da redução de adultos e juvenis. Os valores de triglicéridos foram diferentes entre espécies e a glucose entre épocas, com concentrações mais altas nas Felosas e na migração outonal, respectivamente. A abundância de artrópodes variou para quase todas as ordens entre meses, com valores mais altos no verão. Tal como esperado, o pico de abundância de afídeos coincidiu com o pico de passagem das Felosas, mas a relação entre as duas variáveis não foi significativa. Os itens alimentares mais consumidos por ambos os passeriformes nos dois caniçais foram coleópteros e himenópteros. De acordo com os Índices de Ivlev, houve uma preferência por coleópteros e himenópteros no Paul do Taipal por parte de ambas as espécies e uma preferência por coleópteros, himenópteros, hemípteros e dípteros no Paul da Madriz por parte dos Rouxinóis.

Estes resultados mostram que o Paul do Taipal parece ser um melhor local de paragem devido à elevada abundância e diversidade de itens alimentares e por ser utilizado tanto por Felosas como por Rouxinóis. Os parâmetros ambientais são muito importantes para determinar a duração de paragem destes dois passeriformes. Níveis de metabolitos no sangue estão em conformidade com os Rouxinóis fazerem paragens em Portugal antes e após atravessarem o Mar Mediterrâneo, enquanto as Felosas não parecem engordar nos caniçais portugueses.

Palavras chave: passeriformes do Palearctico, caniçais, estratégias migratórias, stopover

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Chapter 1

Introduction

1.1 - Reed beds as wetlands

The Ramsar Convention defines wetlands as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static, flowing, fresh, brackish or salt, including areas of marine water, the depth of which at low tide does not exceed six meters" (Ramsar Convention Secretariat, 2013). However, due to human action, other types of unnatural wetlands were created such as fish and shrimp ponds, farm ponds, irrigated agricultural land, salt pans, reservoirs, gravel pits, sewage farms and canals. Wetlands are among the richest ecosystems in terms of biodiversity while, paradoxically, one of the most threatened. Besides being cradles of biological diversity and natural habitats for rare or endangered species, wetlands also provide other useful ecological services such as aquifer recharge, improvement and maintenance of water quality and erosion control (Yoon, 2009). They are also important for humans at an economical level by mitigating flood damage, providing timber and other kinds of building materials and harbouring species that can be hunted for food, pelts or sport.

Wetlands are often classified as ecotones, as part of the transition between aquatic and terrestrial environments. Their formation and alteration is linked to the response of the plant community to variable biotic and abiotic factors and is part of an ecological succession from open water to a climax forested ecosystems. This succession may have an autogenic nature, an allogenic nature or, more commonly, a mixture of both (Tansley, 1935). According to the autogenic succession theory, the increasing deposition of vegetable material leads to a decrease in water levels, to the point of achieving the conditions for trees to colonize the area. As more organisms colonize the area, the greater the organic deposition and rate of loss of water due to

evapotranspiration, eventually becoming a terrestrial ecosystem, without external interference.. On the other side, the allogenic succession theory defends that the change in the community through time is not brought by the biota, but is instead an adaptation of the species to the current environment, whose changes alters the community present (Mitsch & Gosselink, 2000).

Wetlands can be classified using two different classification system. One was developed by Cowardin and co-workers (1979) and divided wetlands into five main systems: Marine, Estuarine, Riverine, Lacustrine and Palustrine, corresponding to wetlands situated in or near the coast, estuaries, rivers or lakes, respectively. The Palustrine system includes all other wetlands with a low water salinity and dominance of trees, shrubs or persistent emergent vegetation. Each system was further divided into smaller Subsystems, Classes and Dominance types. However, Cowardin's system did not classify human-made wetlands, such as rice fields and dams. The other classification system was adopted by the Convention on Wetlands in 1990 to correct this deficiency and provide a more comprehensive wetland classification system, the Ramsar Classification System for Wetland Type. This classification divided wetlands into three major categories, Marine/Coastal wetlands, Inland wetlands and Human-made wetlands, each with its own subcategories. Among Cowardin's classification, the Palustrine system includes such wetlands as marshes, bogs, swamps, fens, prairies and reed beds. Reed beds are associations of hydrophyte vegetation that includes species of different families.

1.2 - Biodiversity in reed beds

The most common plant species in reed beds is *Phragmites australis*, commonly known as reed. In optimal conditions, monospecific *P. australis* stands can reach heights of four meters and tends to appear in areas affected by anthropic pressure due to increased concentration of nutrients. It forms extensive stands that grow near lakes, lagoons or rivers with weak streams, although it can tolerate periods without water. It is also tolerant to some degree of salinity, allowing it to occur near estuaries or salt marshes. If not managed regularly, reed beds are bound to disappear sooner or later and give way to scrub or woodland due to its detritus-based nature (Mitsch & Gosselink, 2007). The accumulation of dead vegetation and litter, which consists of shed leaves and standing dead stems, results in the gradual drying of the bed and consequent invasion by scrub or woodland species. Their distribution is wide, as their native range includes Europe and Asia whereas in North America and New Zealand it is considered an invasive species (GISD, 2008). However, there has been significant loss of reed beds throughout Asia and Europe mainly due to agricultural use of land, pollution, rise of sea-level and poor management (Hardman et al., 2012). It is estimated that the area of natural wetlands in the Mediterranean has been reduced to 10%-20% of its original size, and thus so has the area of reed beds been reduced (Martínez-Vilalta et al., 2002).

Reed beds are important, both at economical and ecological levels. They serve as natural filters capable of removing various contaminants such as nitrates, phosphates and dissolved metals, as well as reducing and removing various harmful bacteria from the water (Kern & Idler, 1999). This is because *P. australis* is able to conduct water pollution control underground by use of its roots and rhizomes unlike other nitrophilic marsh plants. Flora and fauna of conservation interest can be found in reed beds,

including rare plants: marsh sow thistle *Sonchus palustris*, marsh pea *Lathyrus palustris*, greater water parsnip *Sium latifolium*, marsh fern *Thelypteris palustris* and crested buckler fern *Dryopteris cristata* (Cowie et al., 1992); a great number of invertebrates (Ditlhogo et al., 1992); and birds of conservation concern in Europe: great bittern *Botaurus stellaris*, moustached warbler *Acrocephalus melanopogon* (Schmidt et al., 2004), aquatic warbler *A. paludicola* and manchurian reed warbler *A. tangorum* (IUCN, 2013). In addition, they are also part of the diet and the natural habitat of specialized fauna such as invertebrates that use the dead stems as a winter refuge (Ostendorp, 1993) and breeding birds that live on the reed beds for protection from predators, nesting and feeding, during and between migrations, including passerines from the *Acrocephalus* genus (e.g.: reed warbler *Acrocephalus scirpaceus*, sedge warbler *A. schoenobaenus*, great reed warbler *A. arudinaceus*), bearded tit *Panurus biarmicus*, and reed bunting *Emberiza schoeniclus* (Baldi & Kisbenedek, 1999; Martínez-Vilalta et al., 2002; Poulin & Lefebvre 2002; Trnka & Prokop, 2006).

1.3 - Migrations of reed bed passerines

Migrations are periodical movements that individuals of several species perform triggered by certain conditions such as season of year, decreased temperatures, lack or reduced food availability or day length (Bibby & Green, 1981; Chernetsov & Manukyan, 1999). These kind of movements have evolved independently in all major animal groups (e.g. mammals, birds, fish, reptiles, amphibians and invertebrates) (Alerstam, Hedenstrom & Akesson, 2003). Migrations are characterized by their annual or seasonal occurrence or movement to a distinct habitat as part of the individual's life history. This allows the differentiation of migrations from other movements such as dispersions, which are short-distance movements between similar or equal habitats, whereas migrations often cover distances not usually travelled by the individuals on a regular basis. There is no consensus in a definition that summarily describes this behaviour but several aspects are required for a journey to be considered a migration, though not all may manifest themselves at a given time.

Persistent movement will take the migrant away from its natural habitat into a new one, allowing the access to some resource not available in its original location and necessary for that organism's life cycle. This movement is normally greater than the distance covered within the organism's original habitat. Secondly, this movement has a straight general direction. Whether the organism has its own means of travelling, like a mammal or bird, or has to rely on external forces in the case of windblown insects and plant seeds, it has at least some degree of control of the direction it is taking. In the latter case insects have the ability of enter or exit winds appropriate for their destination. Third, a migrant ignores certain stimuli during a migration that it would not pass normally. For example, salmon reproduce in the place they were born and only there,

despite possibly finding other suitable places along their journey; migrant birds finding available food sources during their migration will only stop and feed when their energy reserves are depleted. Eventually this behaviour will be suppressed at some point and the migration will come to an end. Fourth, there are distinct behaviours that mark the beginning and end of a migration. As an example, migratory birds rapidly increase their mass and accumulate fat reserves prior to leaving their breeding or wintering grounds while insects focus metabolism to store energy, develop wings in polymorphic species and halt reproductive efforts (Gullan & Cranston, 2004). While sometimes these preparations can seem detrimental because they divert resources from reproduction and growth, they are meant to maximize migratory success and allow organisms to arrive at their destinations in optimal condition. Finally, there is an allocation of energy to support prolonged or extensive movement. Again, an increase in fat reserves can be observed in migrating birds and insects whereas plants accumulate fat in the embryos contained within seeds (Dingle, 1996). This energy allocation is due to the inability of some migrants to replenish their reserves during migration or due to migratory strategies. The purpose of bird migration is to avoid low temperatures, short day length and reduced food availability which occurs in the northern hemisphere where the birds breed (Bibby & Green, 1981).

However, not all organisms have the same patterns of migration. Although the purpose of the migration may vary, all species strive to have successful migrations by maintaining mortality rates as low as possible and reaching their designated location while spending the least amount of time and energy travelling. This objective must take into account such factors as distance travelled, body condition and energy reserves at departure and arrival (Bayly, 2007), timing of departure (Marra et al., 2005), total energy expenditure, wind influence (Akesson & Hedenstrom, 2000) and risk of

predation during the migration. Hence, several migratory strategies have arisen according to each species necessities and adaptations. Generally, migratory birds can adapt their behaviour to achieve one of three possible objectives: have the safest journey possible by reducing mortality rates, the least energetically demanding migration or the fastest migratory journey possible (Akesson & Hedenstrom, 2000). In the case of migratory Palaearctic passerines, four distinct migratory strategies can be found, depending on the birds' increase of body mass during the autumn migration between northern Europe and north Africa: passerines that increase their body mass steadily along the migration route (e.g. garden warbler *Sylvia borin*); passerines that start to increase their body mass sometime after departing and before reaching the Sahara Desert (e.g. *A. schoenobaenus*); passerines that do not present a steady increase in body mass but still accumulate enough reserves to cross the Sahara (e.g. *A. scirpaceus*); and passerines that do not increase their body mass neither accumulate reserves to cross the Sahara, yet stop and refuel in the desert (e.g. spotted flycatcher *Muscicapa striata*) (Yohannes et al., 2008).

Other factors that may influence migrations are environmental parameters. These include climate conditions, such as wind speed, precipitation and cloudiness. Birds often choose to land during adverse weather conditions (Jenni & Schaub, 2003). As for wind, some authors state that it affects passerines' decision of leaving a stopover site, to the point of waiting for a certain period of time and eventually departing if favourable conditions are not met (Akesson & Hedenstrom, 2000; Akesson et al., 2002), while others defend that some passerine species may resume migration regardless of wind direction and assistance, at least for light to moderate tail and headwinds (Bayly, 2007; Karlsson et al., 2011), or regardless of wind direction (Schaub, Liechti & Jenni, 2004). Nonetheless wind characteristics play a crucial part in determining duration and

speed of migration while in flight. Precipitation is also an important environmental factor, because during rain periods flight costs increase due to the detrimental effects of turbulent air, increased weight of wet plumage and lowered visibility (Schaub, Liechti & Jenni, 2004). As such, in conditions of heavy to moderate rain, birds normally stop until conditions are met to continue the migration.

The relationship between atmospheric parameters and their influence on passerine migration can be troublesome to assess given the amount of factors needed to take into account. The use of large-scale climatic phenomena can possibly be used to reduce variability of space and time into simple measures (Stenseth et al., 2003). One of such phenomena is the North Atlantic Oscillation (NAO). The NAO is characterized by an oscillation in atmospheric mass between the subtropic high-pressure zone of Azores and the low-pressure zone of Iceland (Ottersen et al., 2001), and is the most robust pattern of recurrent atmospheric behaviour in the North Atlantic region (Barnston & Livezey, 1987) with greater fluctuations during the winter (Ottersen et al., 2001; Stenseth et al., 2003). The NAO is usually a proxy of northern Europe climate due to its strong relationship with the precipitation, temperature and wind patterns (Ottersen et al., 2001). It is responsible in great part for determining spring and winter temperatures in Europe (Huppopp & Huppopp, 2003) and may vary between positive and negative values. Positive NAO indices translate into stronger winds from the west leading to increased storm activity, temperatures and precipitation in northern Europe, while the contrary occurs in central and south Europe and the Mediterranean region. During negative NAO indices, the patterns are roughly the opposite (Ottersen et al., 2001; Huppopp & Huppopp, 2003; Stenseth et al., 2003). These variations of atmospheric parameters can dictate changes in several aspects of passerine migration such as timing of egg laying (Møller, 2002), presence of favourable winds and food availability before

and during the migration. Another large-scale pattern is the Northern Annular Mode (NAM), also known as Arctic Oscillation. Although very similar to the NAO, the main differences of the NAM are in its spatial pattern, which is centred over the arctic and surrounding latitudes and strong coherence between troposphere and stratosphere while the effects in the North Atlantic zone of a high and low-index NAM are highly correlated with positive and negative NAO indices, respectively (Eichelberger & Holton, 2002). While there is much debate about the possibility of NAO being a regionalization of NAM or totally different paradigms, both indices might have different influences over bird migration.

Long-range migrants often cover distances several thousand times greater in magnitude than their own body length (Alerstam, Hedenstrom & Akesson, 2003). However, such migrants cannot store enough energetic reserves to cover the migration in one bout due to physiological constraints (Schaub & Jenni, 2000). In flying birds, the amount of fuel stored for migration decreases as body mass increases. This fuel is normally stored as fat adipose tissue, an energy-dense substrate (Jenni & Jenni-Eiermann, 1998), which is the most efficient since the costs of transporting these energy reserves are minimal (Alerstam, Hedenstrom & Akesson, 2003). In order to complete their migration, birds need to make periodic stopovers during their migrations, their main purpose being refuelling in order to continue the journey (Chernetsov & Manukyan, 2000; Schaub & Jenni, 2000; Schaub & Jenni, 2001).

1.4 - Evaluating stopover duration during migrations

Stopover usage is dependent on migratory strategies. Migration duration is determined mostly by time spent on stopovers to refuel (Schaub & Jenni, 2000). A high number of quality stopovers equally distributed allows minimization of time spent on migration and early arrival to breeding or wintering sites with fitness improvement. However, due to food preferences, variability in space or time or reduced number of stopover sites, migratory birds need to adapt strategies according to their limitations. While some birds fatten only enough to reach successive periodic stopovers during their migration to refuel their energetic reserves, others decide to gather extensive amounts of fuel to make the same journey in one or two steps. This is related to the distribution of food sources in space and during the migration, and the birds' specific foraging skills (Bibby & Green, 1981). However, stopover quality may vary and birds are thus sometimes forced to feed on alternate food items during migrations (Chernetsov & Manukyan, 2000). The amount of time a migrant will stay at a stopover site depends on its quality. In a good stopover, a bird may stay for as long as it regains enough fuel to reach another stopover or overcome an ecological barrier. If, however, upon arrival at the site it is discovered to be of poor quality or low on food abundance, the time of residence may be as low as one day, after which the bird will depart to find a better spot to refuel. The rate at which a passerine refuels can be assessed by analyzing their fattening rate, the variation in their body mass in a given amount of time. Most studies use the minimum stopover duration which corresponds to the time spent between a consecutive capture and recapture (Schaub & Jenni, 2000). These measurements require the capture of an individual, at least, twice in a short amount of time and may vary significantly due to changes in body mass throughout the period in which the bird

refuels. The problem of the need of such a large recapture effort and the chance of body mass variation derived of stress capture can be solved by using plasma metabolites. The analysis of plasma metabolites such as triglycerides, glucose, glycerol, fatty acids, uric acid and butyrate can be used to assess the instantaneous fuelling rate of an individual from a single capture. The concentration of these metabolites can give valuable information about the body condition of the individual and if it is in the process of fattening or fasting. Triglycerides appear in high amounts during the process of fat deposition or fat mobilization and are synthesized in the liver; during prolonged flight where birds experience fasting and loss of body mass, there is a decrease in glucose, which is the primary energy source, and an increase in fatty acids, glycerol from lipolysis, butyrate from ketone formation and acid uric from protein breakdown (Guglielmo, Cerasale & Eldermire, 2005). According to Minias et al. (2013), hemoglobin concentrations also vary in migratory waders. Since aerobic catabolization of fuel reserves is necessary during flight to provide energy, the oxygen-capacity of avian blood must be adjusted to such needs, depending on the migrant's preferential migratory strategy. Time-minimizing waders accumulate extensive fuel reserves and spend more time in nonstop flight than energy-minimizing migrants and, therefore, are able to increase the blood concentration of hemoglobin prior to departing for a migratory flight. The use of plasma metabolites has some disadvantages though, as it is yet unable to provide but a qualitative measure of mass change without multiple samples (Guglielmo, Cerasale & Eldermire, 2005).

1.5 Aims of this study

The objective of this study was to assess the stopover quality of two reed beds in Central Portugal for two passerine species, *Acrocephalus scirpaceus* (Reed Warbler) and *Acrocephalus schoenobaenus* (Sedge Warbler), similar in physiology but with contrasting migratory strategies. Firstly the influence of environmental variables on stopover duration and body weight variation was evaluated using 10 years of regular ringing data. Secondly, the health condition of individuals was assessed using body condition as a proxy and blood metabolites to assess possibility of refueling stopover. Although several authors have different meanings for body condition (e. g. Akesson et al., 2002), in this study it is considered as the relationship between wing length and body weight. Thirdly, a quantitative analysis of the invertebrate fauna on the two sites was used to describe abundances of prey and the peak of passage of Sedge Warblers was compared with the peak of abundance of their preferred food item described in the literature, *Hyalopterus prunis* aphids. Finally, the abundance of the most representative arthropod orders in the environment were compared with their presence in the diet of both study species to determine preferred items or specialization.

Chapter 2

Materials & Methods

2.1 - Study sites

Data was collected in two wetlands situated in the Lower Mondego Valley in central Portugal: Paul do Taipal and Paul da Madriz. Paul do Taipal (40°11'N 008°41'W) is a Special Protection Area (SPA) under EEC Birds Directive 79/409/EEC (Decreto-lei n° 384-B/99 on 23th of September) and considered a Wetland of International Importance (WII) by the Ramsar Convention on Wetlands. Spanning across 233 ha with a minimum of 3 and maximum of 25 m of elevation, this inland wetland is composed of seasonal and permanent freshwater pools with extensive reed beds and irrigation channels and rice fields downstream. The channels were once used to drain the marsh for agricultural purposes but this practice was abandoned in the 1970's. *P. australis* forms its extensive reed beds with *Typha latifolia* and *Scirpus lacustris* in deeper waters and about 200 species of hydrophytic species along the channels. It holds a great bird diversity and is important for some fish species as well as a resting and wintering stage for migratory birds, specially migratory passerines (e.g. *A. scirpaceus*, *A. schoenobaenus* and *Luscinia svecica*). This wetland also presents several species of fish, birds and mammals present in the Red Data list of Vertebrates for Portugal.

Paul da Madriz (40°08'00"N 008°38'00"W) is also a SPA under Article 4 of the EC Wild Birds Directive (79/409), with an area of 226 ha and between 8 and 61 m of elevation, respectively. It is a mixed habitat of riparian and palustrine (*P. australis*) characteristics with a permanent water table. This wetland is an important site for breeding mallard *Anas platyrhynchos* and other wintering waterfowl species as well as *Ixobrychus minutus*, *Cettia cetti*, *A. arundinaceus* and *A. scirpaceus*.



Figure 1 - Mist net at Paul do Taipal. Photo courtesy of Miguel Araújo.

2.2 - Study species

Two migratory insectivore passerines were chosen for this study: the Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *A. schoenobaenus*. The reasons behind this choice were the physiologic similarity between both species as well as choice in stopover habitat that contrasted with different feeding habits and migratory strategies.

The Reed Warbler is a common, medium-sized migratory insectivore territorial passerine (Bibby & Green, 1981; Péron et al., 2007). Widespread across all Europe, breeds in middle latitudes of west Palearctic with central European and southern Sweden prevalence and presents a patchy distribution around the Mediterranean (Cramp, 1992). The Reed Warbler's natural habitat are reed beds (Poulin et al., 2002), where it feeds on small invertebrates which occur predictably in low densities (Bibby & Green, 1981; Schaub & Jenni, 2000). An opportunist generalist, also feeding on small snails and occasionally on plant material (Cramp, 1992), it hunts mainly in lower and upper reeds (Bibby & Green, 1983). This species breeds in Europe and winters in sub-Saharan Africa. Juveniles migrate later than adults and their migration takes typically more time, since more time is spent on stopovers refuelling (Rguibi-Idrissi, Julliard & Bairlein, 2003) and stopover duration is the most important factor in the determination of overall migration speed (Schaub & Jenni, 2001). Spring migration from the wintering to the breeding sites takes place during March-May; the inverse autumn migration occurs during July-October. Reed Warbler's migration is characterized by short bouts of flight alternating with long stopovers to refuel for another stage of flight.

Contrarily, the Sedge Warbler is an aphid specialist. Its distribution extends from high arctic down to mid-latitudes and beyond the west Palearctic (Cramp, 1992). It has

a preference for drier habitats compared to the Reed Warbler although it still frequents reed beds. Analogous to Reed Warbler, it also winters south of the Sahara desert, feeding extensively on plum-reed aphids *Hyalopterus prunis*, a rich but highly unpredictable prey, available in southern Britain and northern France, where it feeds intensively to accumulate enough energetic reserves to cross the Sahara desert without stopping to refuel. This way, the Sedge Warbler can cover the same distance as the Reed Warbler in less time, since the Reed Warbler needs to refuel two or three times to complete the same journey (Bayly, 2007). The rest of the time it feeds mostly on slow, soft-bodied prey (Cramp, 1992).

2.3 - Bird ringing

At each study site mist nets were erected before dawn and operated for five hours after sunrise. This was done on two non consecutive days every week during spring migration (15th March - 30th April) and autumn migration (1st August - 15th October). Captured birds were ringed, aged and sexed, whenever possible. Morphological parameters such as wing-length, bill-length, tail-length, tarsus-length and body mass were obtained according to Svensson (1992). Minimum stopover duration was determined by calculating the number of days passed between the first capture of an individual and its last recapture (Chernetsov, 2012). Birds captured only once were excluded from this study. It was assumed that birds did not leave the sites between the first and the last capture event if captured within the ringing periods considered.

2.4 - Faecal samples

To evaluate the diet of the birds, faecal samples were collected whenever possible from bags where the individuals were kept for up to 30 minutes prior to ringing. The faeces were scrapped into an eppendorf and stored in a 80% alcohol solution. They were later observed under an optical microscope and diet remains were identified to order using comparisons made with samples of arthropods collected in the field. A total of 483 faecal samples were collected from Reed Warbler, of which 244 contained identifiable arthropod remains, while the rest contained none or some remains that were impossible to identify. Of 41 Sedge Warbler faeces, 19 yielded usable samples.

2.5 - Arthropod sampling

To determine food abundance in each site, arthropod counting was conducted during and between both migration seasons in 2012. Randomly selected *P. australis* reeds, distanced approximately 10 meters apart, along a 100 meters transect besides the mist net line, were inspected for arthropods on the stem and on leaves (above and below). Counting was performed at the end of the scheduled ringing sessions, between approximately 9 and 12 am. Relative abundance of arthropods was compared with the diet of each bird species using the Ivlev Index (Strauss, 1979).

2.6 - Blood sampling

A blood sample (ca 75 μ l) was collected from the first two captured individuals of each species each session. Samples were taken from the brachial vein into heparinized micro-haematocrit capillary tubes, and used immediately to measure triglycerides and glucose concentrations in the blood using portable instruments (Triglycerides: Roche Accutrend GCT – precision 50- 500 mg/dL (0.80-6.86 mg/dL); Glucose: Roche *Accu-Check Advantage* – precision 30 – 345mg/dL(+/- 5 mg/dL)).

2.7 - Statistical analyses

Statistical analyses were carried out using Statistica v. 7 (Statsoft, Tulsa, USA) and program R (Crawley, 2007). Data from 13 years of ringing was used to verify the existence of significant differences in the number of birds of each species between the two study sites. Number of captures was transformed to reflect the number of individuals caught by hour by meter of net in each month. Because there was no homogeneity of variances in the data, non-parametric Mann-Whitney U tests were performed to test for differences in capture rate between sites.

Several environmental parameters were used to explain stopover duration and average body weight variation. Body weight variation corresponded to the difference in weight between the capture on an individual and its last recapture during a migration season. The environmental parameters used were: NAO monthly values, NAO and NAM values from December to March and from April to June and wind speed and precipitation values in Portugal, Central Europe and North Africa.

NAO and NAM are atmospheric patterns indices used as proxy of North Atlantic weather. Winter months are more pronounced in the NAO index, with fluctuations that have repercussions throughout the rest of the year. Thus, NAO indices for winter can be used for to assess the influence on the coming months (Stenseth et al., 2003). Wind speed and precipitation are environmental factors that birds take into account when deciding when to leave a stopover site and influence their decision to resume migration (Akesson & Hedenstrom, 2000; Schaub, Liechti & Jenni, 2004). Data from Central Europe was used due to the relative high number of individuals with French rings captured in our study site (pers. observations), possibly indicating their main path to transverse the Mediterranean and North Africa. Each variable was used in an univariate General Linear Model to assess its importance in explaining stopover duration and weight variation during both migrations between 2000 and 2012.

Two-way ANOVAs were used to evaluate the effect of season, year and their interaction on body condition of both study species and the effect of species, both migrating seasons and their interaction on triglycerides and glucose levels.

Reed Warbler productivity, the ratio between juveniles and adults in given time, was calculated for each year between 2000 and 2012 in Paul do Taipal.

Two-way ANOVAs followed by post-hoc Tukey tests were used to test for possible relationships between the effect of site, month and their interaction on the log-transformed abundance of each representative arthropod order. *H. prunis* aphids were also compared as they appear extensively in the Sedge Warbler's diet in Western Europe (Bibby & Green, 1981) and a Spearman Correlation was used to assess if there was a match between the peak of abundance of Sedge Warblers and aphids.

The percentage of occurrence of each arthropod taxa, representative in the environment, and present in the birds' diet was calculated and used to determine the

Ivlev Index. The Ivlev Electivity Index (E) determines the degree of selection of a specific prey in the environment by a given predator. It is given by the equation $E = \frac{r_i - p_i}{r_i + p_i}$, where E is the measure of electivity, r_i is the relative abundance of prey i in the gut of the predator and p_i is the relative abundance of the same prey in the environment (Strauss, 1979). E can vary between -1 (avoidance or inability to hunt prey) or 1 (active search and hunt of prey). Again, *H. prunis* aphids were also compared due to their high importance in the Sedge Warbler diet.

Finally, differences in the proportion of faecal samples with each one of the main items in the diet were compared between sites with a Chi-square test.

Chapter 3

Results

3.1 - Ringing data

3.1.1 - Determination of peak of passage

As shown in Figure 2, capture rate of adult Reed Warblers was much higher in Paul do Taipal than Paul da Madriz, and a similar pattern was registered for juveniles (Figure 3). Captures of Sedge Warbler present a similar trend to that of the Reed Warbler, despite smaller discrepancy. However, overall capture rates were much lower than those of Reed Warblers. A single adult was captured in May, outside the window of the spring migration (Figure 2). Captures were more numerous during the autumn migration (from July until September for adults, October for juveniles) with the peak of passage for adults in July. Numbers decreased sharply in the following months. As for Paul da Madriz, captures were notoriously lower for all ages.

Juvenile Reed Warbler peak of passage was in July. Contrary to adults, juvenile captures in Paul do Taipal did not decrease so abruptly, with quite similar captures in August and September, before a large decrease in October. No Sedge Warbler juveniles were captured at Paul da Madriz and two small peaks of abundance were presented in July and September (Figure 3).

Mann-Whitney U tests showed a significant difference in Reed Warblers between Paul do Taipal and Paul da Madriz for both adults ($Z = 5.7$; $p < 0.001$) and juveniles ($Z = 7.58$; $p < 0.001$). The test was not performed for Sedge Warbler due to the lack of individuals captured at Paul da Madriz.

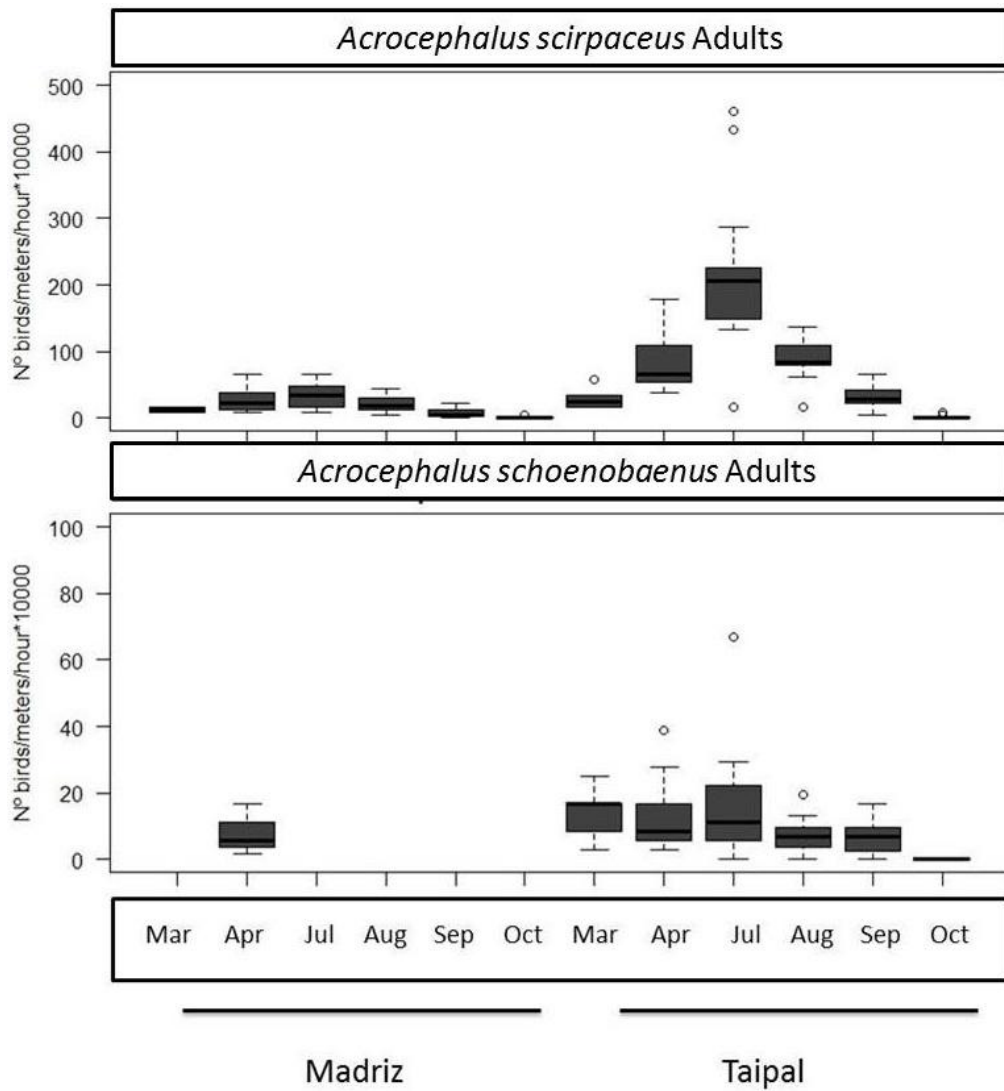


Figure 2 - Adult Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus* caught between 2000 and 2012 in Paul do Taipal and Paul da Madriz during spring and autumn migration. Thick black line = median; dark grey boxes = 25-75% inter-quartile range; dotted line = non-outlier range; open circles = outliers.

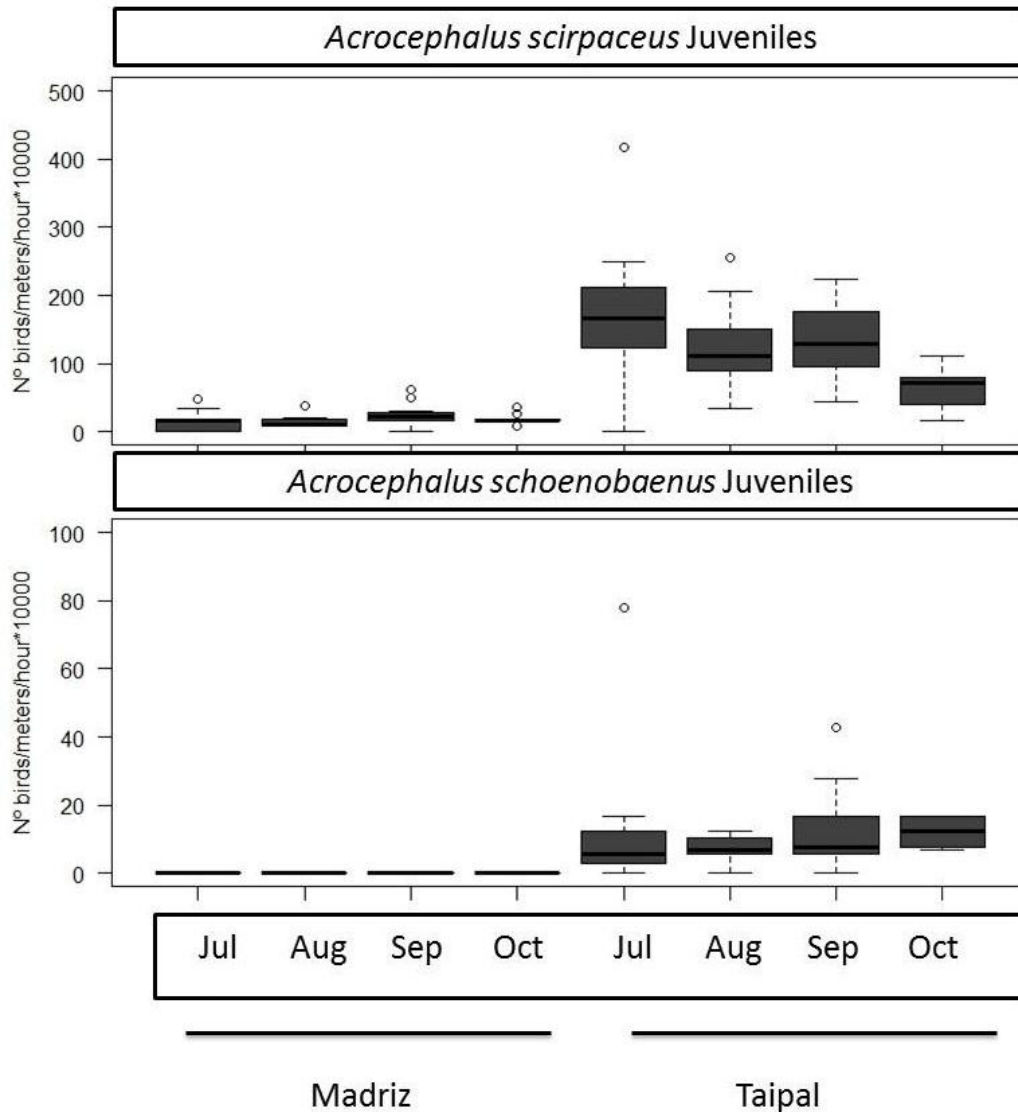


Figure 3 - Juvenile Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *Acrocephalus schoenobaenus* caught between 2000 and 2012 in Paul do Taipal and Paul da Madriz during autumn migration. Thick black line = median; dark grey boxes = 25-75% inter-quartile range; dotted line = non-outlier range; open circles = outliers.

3.1.2 - Influence of environmental factors

Table I - Average stopover duration and body weight variation with standard deviation of Reed Warbler *Acrocephalus scirpaceus* during spring and autumn migration between 2000 and 2012.

Reed Warbler <i>Acrocephalus scirpaceus</i>			
Spring migration		Autumn migration	
Stopover duration	Body weight variation	Stopover duration	Body weight variation
17.85 ± 16.68 (n = 116)	-0.058 ± 1.39 (n = 116)	17.46 ± 16.55 (n = 544)	0.42 ± 1.44 (n = 544)

Table II shows the results of the univariate GLM used to explain average stopover days and body weight variation during the spring migration of Reed Warbler using several environmental parameters. All parameters showed great influence on stopover days ($p < 0.05$), except for monthly NAO values (Table II). As for average body weight variation, it was not influenced by as many parameters and monthly NAO values were also not significant (Table II). During the autumn migration, the pattern was the same for stopover duration, as the same parameters were influential ($p < 0.001$) while the factors which influenced variation of body weight were wind speed in Portugal and Central Europe, monthly NAO values and NAO values between August and October (Table III).

Table II - Results of the univariate General Linear Model using environmental parameters to explain mean stopover days and body weight variation of Reed Warbler *Acrocephalus scirpaceus* during the spring migration between 2000 and 2012. For definition of mean stopover days and body weight variation see text.

Spring Migration of Reed Warbler <i>Acrocephalus scirpaceus</i>						
	Average stopover duration			Average body weight variation		
	df	t	p	df	t	p
December-March NAO	122	-5.16	< 0.001	122	2.43	0.02
December-March NAM	122	-5.03	< 0.001	122	2.24	0.03
Precipitation Portugal	122	4.05	< 0.001	122	-1.94	0.05
Wind speed North Africa	122	3.81	< 0.001	122	-1.48	0.14
Precipitation North Africa	122	3.63	< 0.001	122	-2.01	< 0.05
Wind speed Portugal	122	2.06	0,04	122	-0.41	0.68
Monthly NAO	122	-1.31	0,19	122	1.67	0.1

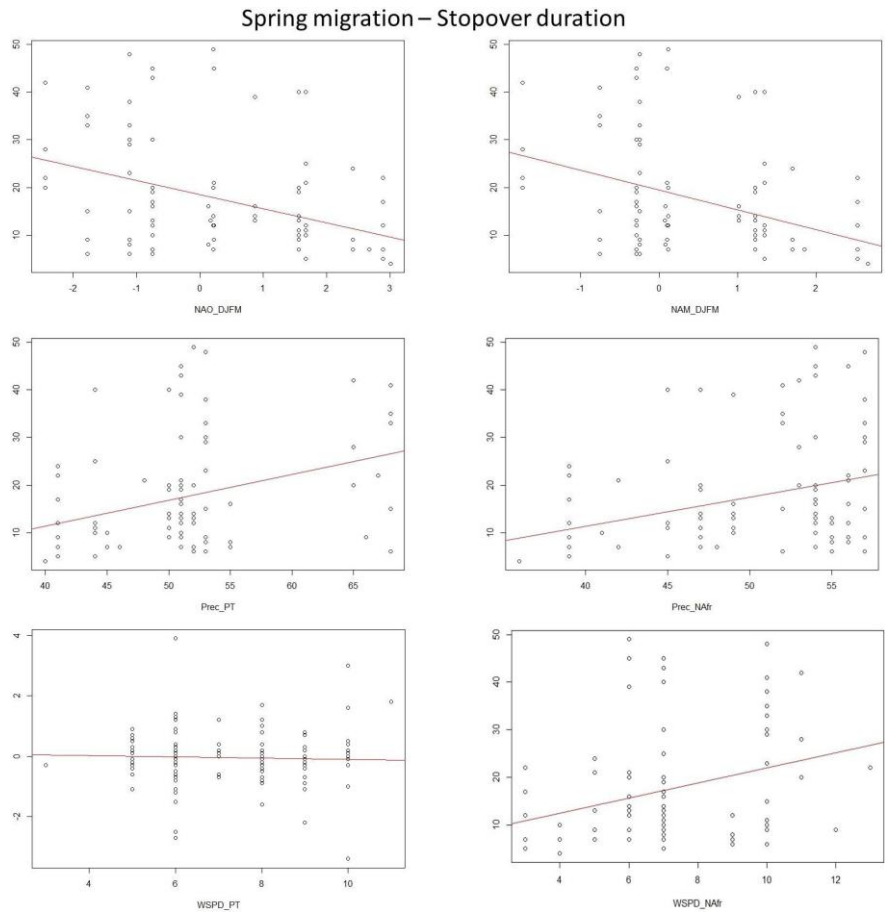


Figure 4 - Graphic representation of the six most significant environmental parameters used in the univariate General Linear Model used to explain stopover duration during the spring migration between 2000 and 2012.

Spring migration - Body weight variation

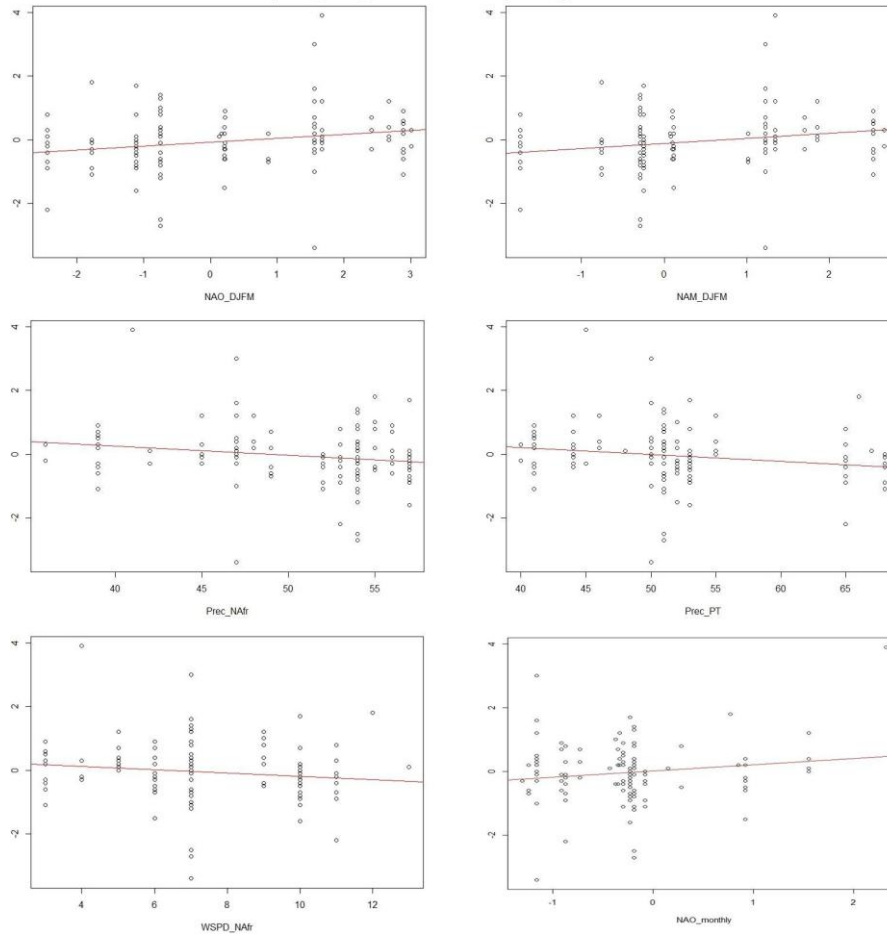


Figure 5 - Graphic representation of the six most significant environmental parameters used in the univariate General Linear Model used to explain body weight variation during the spring migration between 2000 and 2012.

Table III - Results of the univariate General Linear Model using environmental parameters to explain average stopover days and body weight variation of Reed Warbler *Acrocephalus scirpaceus* during the autumn migration between 2000 and 2012. For definition of mean stopover days and body weight variation see text.

Autumn Migration of Reed Warbler <i>Acrocephalus scirpaceus</i>						
	Average stopover duration			Average body weight variation		
	df	t	p	df	t	p
December-March NAO	531	-7	< 0.001	531	-0.58	0.56
December-March NAM	531	-6.77	< 0.001	531	-0.25	0.8
Precipitation Central Europe	531	-6.2	< 0.001	531	-1.57	0.12
Wind speed Portugal	531	5.45	< 0.001	531	3.16	< 0.005
August-October NAO	531	-5.1	< 0.001	531	-2.51	0.01
Wind speed Central Europe	531	-4.82	< 0.001	531	-2.15	0.03
Precipitation Portugal	531	3.92	< 0.001	531	1.36	0.17
Monthly NAO	531	0.23	0.82	531	-2.74	0.01

Autumnal migration – Stopover duration

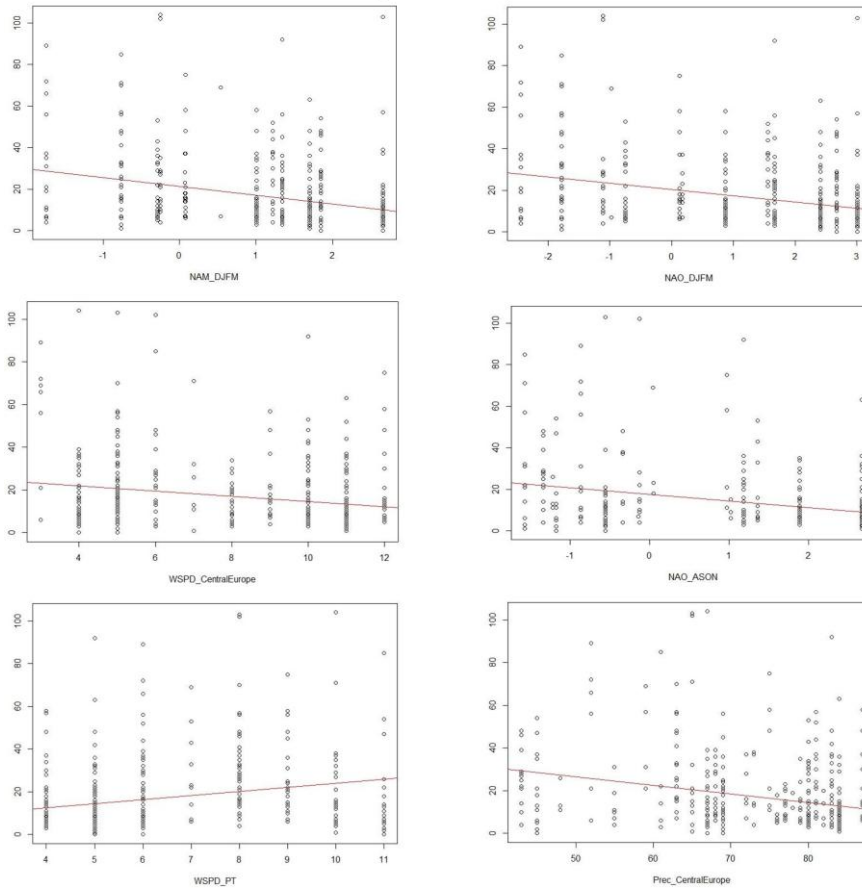


Figure 6 - Graphic representation of the six most significant environmental parameters used in the univariate General Linear Model used to explain stopover duration during the autumn migration between 2000 and 2012.

Autumnal Migration – Body weight variation

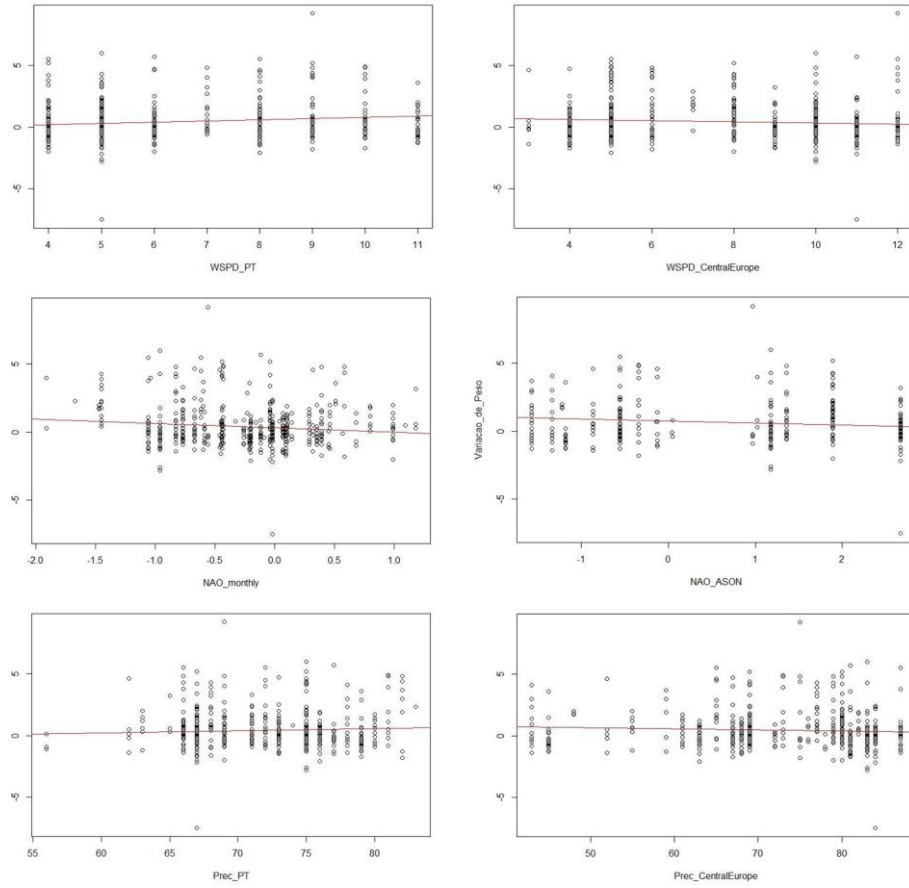


Figure 7 - Graphic representation of the six most significant environmental parameters used in the univariate General Linear Model used to explain body weight variation during the autumn migration between 2000 and 2012.

3.1.3 - Body condition variability

Table IV presents the values of the mean body condition of adult and juvenile Reed Warbler and Sedge Warbler and their respective standard deviations during the spring migration, breeding season (for the Reed Warbler) and autumn migration. The values were compared with a Two-Way ANOVA which shows that significant differences ($p < 0.001$) were found only between seasons (Table V). The results for the Two-Way ANOVA evaluating the effect of age class (adults and juveniles), season (spring migration, breeding and autumn migration) and their interaction (age class*season) on body condition of Reed Warblers are presented in Table VI. The two-way ANOVA results revealed significant differences ($p < 0.001$) not only in season and age, but also in the interaction between these two factors (Table VI). A post-hoc Tukey HSD test showed significant differences between breeding and autumn migration and spring and autumn migrations. As for the interaction between season and age class, significant differences were found between spring and autumn migration in adults and between the autumn migration of adults and juveniles.

Table IV - Average body condition values with standard deviation of Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *Acrocephalus schoenobaenus* during each season from 2000 to 2012. For definition of body condition see text.

	Body condition			
	Reed Warbler		Sedge Warbler	
	Adult	Juvenile	Adult	Juvenile
Spring migration	-0.29 ± 1.23 (n = 521)	-	0.64 ± 1.87 (n = 43)	-
Breeding	-0.35 ± 1.22 (n = 973)	-0.26 ± 1.23 (n = 418)	-	-
Autumn migration	0.56 ± 1.23 (n = 771)	-0.19 ± 1.23 (n = 1475)	1.41 ± 1.85 (n = 109)	1.04 ± 1.85 (n = 131)

Table V - Two-way ANOVA evaluating the effect of season (spring migration, breeding and autumn migration), year and their interaction on body condition of Reed Warbler *Acrocephalus scirpaceus*.

Body Condition of Reed Warbler <i>Acrocephalus scirpaceus</i>			
	df	F	p
Season	2	68.20	< 0.001
Year	12	2.22	0.14
Season*Year	2	0.61	0.55

Table VI - Two-way ANOVA evaluating the effect of season (spring migration, breeding and autumn migration), age class (adults and juveniles) and their interaction on body condition of Reed Warbler *Acrocephalus scirpaceus*.

Body Condition of adult and juvenile Reed Warbler <i>Acrocephalus scirpaceus</i>			
	df	F	p
Season	2	71.54	< 0.001
Age	1	120.51	< 0.001
Season*Age	1	111.94	< 0.001

Table VII - Two-way ANOVA evaluating the effect of season (spring and autumn migration), year and their interaction on body condition of Sedge Warbler *Acrocephalus schoenobaenus*.

Body condition of Sedge Warbler <i>Acrocephalus schoenobaenus</i>			
	df	F	p
Season	1	5.25	< 0.01
Year	12	0.52	0.47
Season*Year	1	3.47	0.03

As shown in Table VII, a two-way ANOVA shows significant differences of Sedge Warbler body condition among seasons ($p < 0.01$) and also an interaction between season and year ($p = 0.03$).

3.1.4 - Reed Warbler productivity

Figure 8 shows the productivity of Reed Warbler in Paul do Taipal between 2000 and 2012. There is a trend for an increasing productivity in the last years, albeit with a decrease between 2006 and 2008, translating in an increasing proportion of juveniles compared to the number of adults in Paul do Taipal.

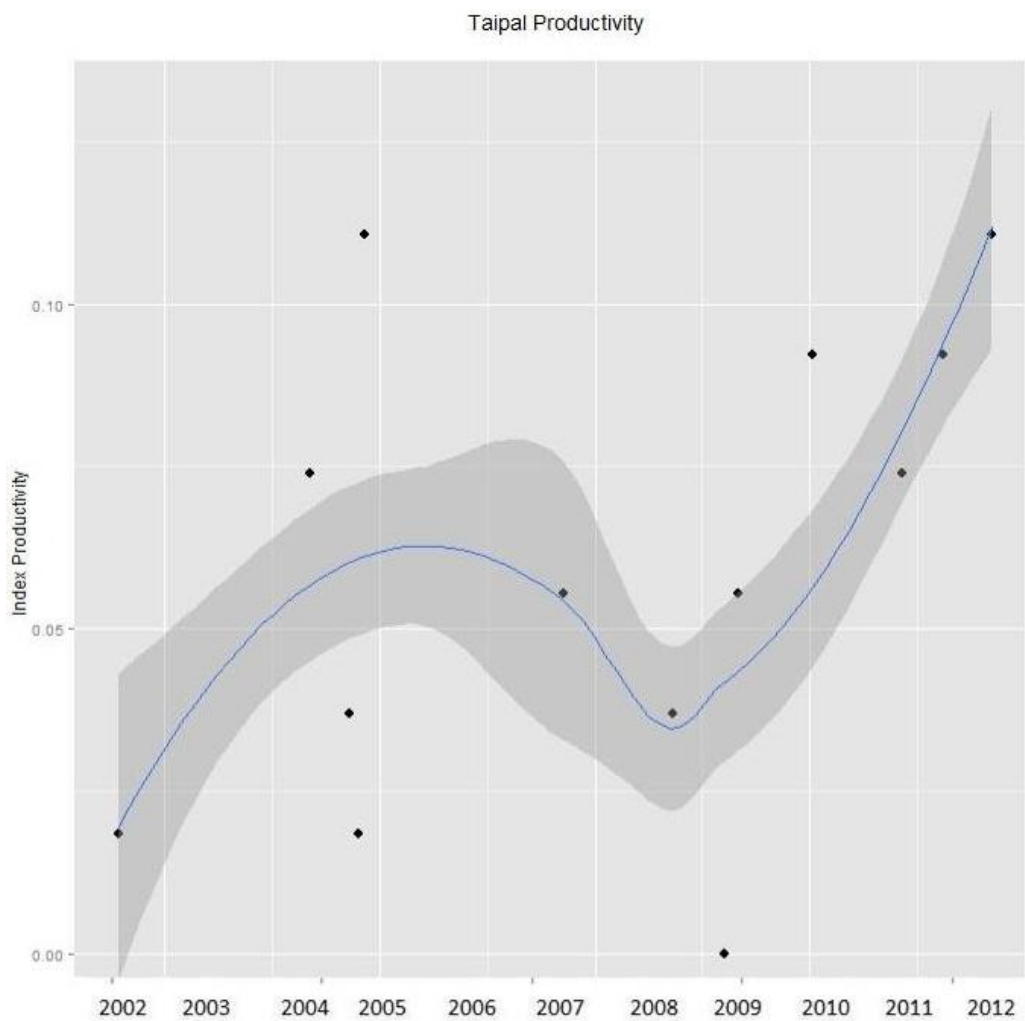


Figure 8 - Productivity of Reed Warbler *Acrocephalus scirpaceus* in Paul do Taipal between 2000 and 2012. Blue line = mean; dark grey area = confidence interval 95%; black dots = scores.

3.1.5 - Blood metabolites

The comparison of triglycerides and glucose levels between Reed Warbler and Sedge Warbler is shown in table IX. The number of individuals sampled were greater during the autumn migration than the spring migration for both species (Table VIII). Significant differences were found in triglycerides levels between both species ($p < 0.001$) and in glucose levels between both migration seasons ($p < 0.001$, Table IX).

Table VIII - Average triglycerides and glucose values with standard deviation in Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *Acrocephalus schoenobaenus* measured in 2012 during each season. Values expressed in mg/dL.

	Acrocephalus scirpaceus		Acrocephalus schoenobaenus	
	Triglycerides	Glucose	Triglycerides	Glucose
Spring migration	151.61 ± 91.24 (n = 78)	311.48 ± 74.68 (n = 81)	264.09 ± 131.45 (n = 17)	247.86 ± 63.54 (n = 15)
Breeding	117.18 ± 70.63 (n = 82)	258.03 ± 70.63 (n = 80)	-	-
Autumn migration	258.03 ± 43.14 (n = 117)	246.18 ± 36 (n = 128)	277.44 ± 115.45 (n = 59)	239.36 ± 50.04 (n = 75)

Table IX - Comparison of blood metabolites (triglycerides and glucose) between Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *Acrocephalus schoenobaenus* and seasons (spring and autumn migration).

	Triglycerides			Glucose		
	df	F	p	df	F	p
Species	1	98,84	< 0.001	1	5,23	0,023
Season	1	0,02	0,88	1	50,6	< 0.001
Species*Season	1	1,75	0,187	1	2,53	0,11

3.2 -Prey abundance

3.2.1 - Inter-site variability

Table X and XI show the average abundance of arthropod orders counted in Paul do Taipal and Paul da Madriz, respectively. Aphids were, by far, the arthropod most found, despite being present only between May and September. While Paul da Madriz presented the most abundance (Table XI), aphids were found in more months in Paul do Taipal (Table X). Araneae was the order most present, appearing in all months, except for May and July in Paul da Madriz (Tables X and XI).

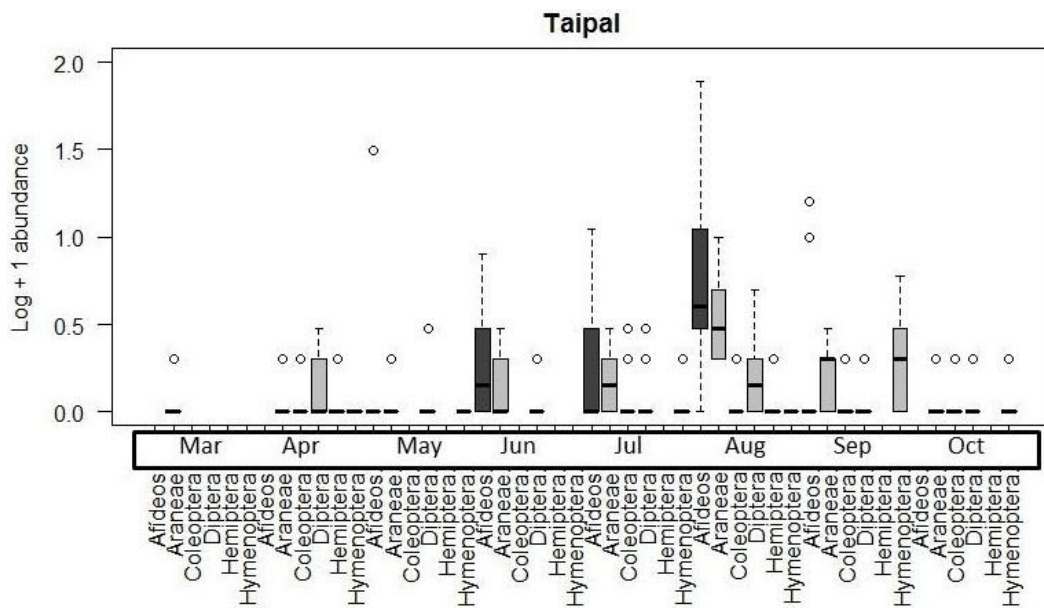


Figure 9 - Graphic representation of abundance of arthropod orders in Paul do Taipal between 2000 and 2012. Thick black line = median; grey boxes = 25-75% inter-quartile range; dotted line = non-outlier range; open circles = outliers.

Table X - Average abundance with standard deviation of arthropod orders counted in Paul do Taipal between March and October of 2012

	Paul do Taipal									
	March	April	May	June	July	August	September	October		
Araneae	0.1 ± 0.32 (n = 1)	0.025 ± 0.16 (n = 1)	0.1 ± 0.32 (n = 1)	0.5 ± 0.71 (n = 5)	0.35 ± 0.67 (n = 7)	0.58 ± 1.47 (n = 29)	0.2 ± 0.46 (n = 8)	0.05 ± 0.22 (n = 1)		
Coleoptera	-	0.05 ± 0.22 (n = 2)	-	-	0.3 ± 0.37 (n = 3)	0.04 ± 0.2 (n = 2)	0.025 ± 0.1 (n = 1)	0.05 ± 0.22 (n = 1)		
Diptera	-	-	-	-	-	0.02 ± 0.14 (n = 1)	-	-		
Diptera	-	0.15 ± 0.48 (n = 6)	0.2 ± 0.6 (n = 2)	0.1 ± 0.32 (n = 1)	0.15 ± 0.49 (n = 3)	0.18 ± 0.66 (n = 9)	0.025 ± 0.16 (n = 1)	0.1 ± 0.31 (n = 2)		
Gastropoda	-	-	-	-	0.05 ± 0.22 (n = 1)	0.02 ± 0.14 (n = 1)	-	0.05 ± 0.22 (n = 1)		
Hemiptera*	-	0.025 ± 0.16 (n = 1)	-	-	-	0.02 ± 0.14 (n = 1)	-	-		
Hymenoptera	-	-	-	-	0.05 ± 0.22 (n = 1)	-	0.325 ± 0.76 (n = 13)	0.05 ± 0.22 (n = 1)		
Isopoda	-	0.025 ± 0.16 (n = 1)	-	-	0.05 ± 0.22 (n = 1)	-	-	-		
Aphids	-	-	3 ± 9.49 (n = 30)	1.4 ± 2.22 (n = 14)	0.85 ± 2.46 (n = 17)	3.48 ± 11.57 (n = 174)	0.6 ± 2.11 (n = 24)	-		

*except aphids

Table XI - Average abundance with standard deviation of arthropod orders counted in Paul da Madriz between March and October of 2012

	Paul da Madriz									
	March	April	May	June	July	August	September	October		
Araneae	0.1 ± 0.32 (n = 1)	0.075 ± 0.35 (n = 3)	-	0.3 ± 0.48 (n = 3)	-	0.42 ± 0.75 (n = 21)	0.17 ± 0.46 (n = 5)	0.2 ± 0.52 (n = 4)		
Coleoptera	-	0.05 ± 0.22 (n = 2)	-	-	-	0.02 ± 0.14 (n = 1)	-	0.05 ± 0.22 (n = 1)		
Diptera	-	-	-	0.1 ± 0.32 (n = 1)	-	-	-	-		
Diptera	-	-	0.1 ± 0.45 (n = 2)	-	-	0.12 ± 0.39 (n = 6)	-	-		
Gastropoda	-	-	-	-	-	-	-	-		
Hemiptera*	-	-	-	-	-	-	-	-		
Hymenoptera	-	0.125 ± 0.65 (n = 5)	0.05 ± 0.22 (n = 1)	-	-	0.04 ± 0.2 (n = 2)	0.17 ± 0.38 (n = 5)	0.05 ± 0.22 (n = 1)		
Isopoda	-	-	-	-	-	-	-	-		
Aphids	-	-	2.05 ± 4.51 (n = 41)	7.2 ± 14.01 (n = 72)	-	7.16 ± 15.52 (n = 304)	-	-		

*except aphids

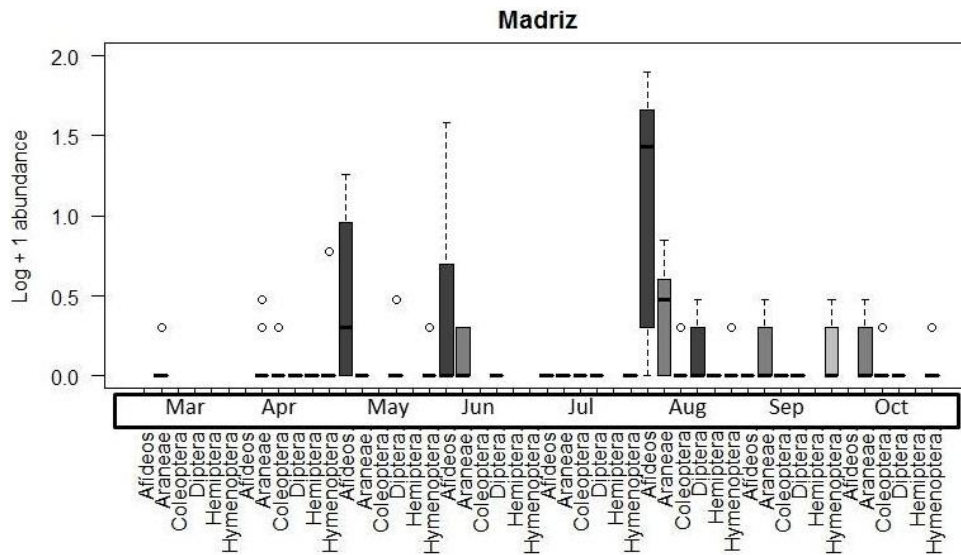


Figure 10 - Graphic representation of abundance of arthropod orders in Paul do Taipal between 2000 and 2012. Thick black line = median; grey boxes = 25-75% inter-quartile range; dotted line = non-outlier range; open circles = outliers.

Table XII presents a two-way ANOVA indicating significant differences among months (all values of $p < 0.001$, except for Coleoptera) for the four most abundant orders, Araneae, Coleoptera, Diptera and Hymenoptera and also aphids. No significant differences were found for site effect, apart from Diptera, and there was no interaction between site and month (Table XII). A post hoc Tukey HSD test showed that significant differences in Araneae abundance were found during August for both sites ($p < 0.04$). As for Diptera, all significant differences were found for August in Paul do Taipal ($p < 0.04$). In the case of Hymenoptera, significant differences ($p < 0.007$) occurred between September in Paul do Taipal and all other effects ($p < .01$), save for September in Paul da Madriz ($p = 0.2$). Finally, aphids present all meaningful differences during August in Paul da Madriz ($p < 0.05$).

Table XII - Two-way ANOVA results for each representative arthropod order in both sites.

Values in bold represent significant differences.

	Araneae			Coleoptera			Diptera			Hymenoptera			Aphids		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Site	1	3.23	0.07	1	1.68	0.2	1	6.4	0.01	1	0.01	0.9	1	0.39	0.53
Month	7	16.41	< 0.001	4	0.5	0.74	6	3.74	< 0.005	5	6.99	< 0.001	4	11.61	< 0.001
Site*Month	7	1.55	0.15	4	0.45	0.77	6	0.67	0.67	5	2.04	0.08	4	1.57	0.19

3.2.2 - Temporal overlap of Sedge Warbler *Acrocephalus schoenobaenus* and

Hyalopteris prunis aphids

A Spearman Correlation was used to determine if there was an overlap of both peaks of abundance of Sedge Warbler and *Hyalopteris prunis* aphids. No significant differences were found ($r = -0.12$, $t = -0.47$, $p = 0.64$), which translates in both peaks of abundance appearing at similar times but the relationship between the two variables not being significant.

3.3 - Reed and Sedge Warbler Diet

3.3.1 - Occurrence of arthropods in faecal samples

Reed Warbler consumed mostly Coleoptera and Hymenoptera in Paul do Taipal (% of occurrence >50 for most of the year, Table XIII). Araneae were also an important item in their diet as they appear in faecal samples in every month, although with a lower proportion (Table XIII). The trend was similar for Paul da Madriz, with Coleoptera and Hymenoptera as the most important items (% of occurrence ≥ 50 throughout the year, except for April and February in the former and April in the latter), but also with an increased importance of Diptera and Hemiptera, present in seven and five months respectively, while Araneae was less important (% of occurrence ≤ 50 in a total of six months) (Table XIII). A single seed was found in a sample in Paul da Madriz (Table XIV). In all faecal samples there were pieces too digested to be identified.

Table XIII - Percentage of occurrence of each order of arthropods in the faeces of Reed Warbler

Acrocephalus scirpaceus collected in Paul do Taipal.

	2011			2012						
	June	August	September	March	April	June	July	August	September	October
n	1	13	5	3	17	13	59	39	18	4
Araneae	-	15.38	40	33.33	11.76	7.69	11.86	17.95	50	75
Coleoptera	100	46.15	100	33.33	23.53	53.85	59.32	56.41	77.78	75
Diptera	-	-	-	-	76.47	-	15.25	20.51	27.78	25
Hemiptera*	-	-	-	-	-	-	5.08	7.69	11.11	-
Aphids	-	7.69	-	-	-	7.69	-	2.56	-	-
Hymenoptera	100	69.23	40	66.67	88.24	76.92	88.14	71.79	72.22	75
Neuroptera	-	-	-	-	-	-	-	-	-	-
Odonata	-	-	-	-	-	-	16.95	15.38	33.33	-
Thysanoptera	-	-	-	-	-	-	-	2.56	-	-
Psocoptera	-	-	-	33.33	-	-	1.69	7.69	-	-
Seeds	-	-	-	-	-	-	-	-	-	-
Other**	100	100	100	100	100	100	100	100	100	100

*except aphids

**pieces too worn out to identify

Table XIV - Percentage of occurrence of each order of arthropods in the faeces of Reed Warbler

Acrocephalus scirpaceus collected in Paul da Madriz.

	2011		2012							
	April	August	February	March	May	June	July	August	September	October
n	1	2	1	2	6	10	5	33	9	3
Araneae	-	50	-	50	-	10	-	21.21	22.22	33.33
Coleoptera	-	100	-	50	100	90	60	78.79	77.78	100
Diptera	100	-	100	-	16.67	50	-	33.33	44.44	66.67
Hemiptera*	-	-	-	50	16.67	10	20	12.12	-	-
Aphids	-	50	-	-	-	-	-	-	-	-
Hymenoptera	-	100	100	50	50	70	80	63.64	77.78	66.67
Neuroptera	-	-	-	50	-	-	-	-	-	-
Odonata	-	-	-	-	-	-	-	12.12	22.22	-
Thysanoptera	-	-	-	-	-	-	-	-	-	-
Psocoptera	-	-	-	-	-	-	-	-	-	-
Seeds	-	-	-	-	-	-	-	-	-	33.33
Other**	100	100	100	100	100	100	100	100	100	100

*except aphids

**pieces too worn out to identify

Coleoptera and Hymenoptera also seemed to be the most important items for the Sedge Warbler, with Hymenoptera appearing in the diet during both migration seasons in percentages higher than 50%, and Coleoptera present between July and September in percentages ≥ 83.33 (Table XV). These results may be biased due to the low number of samples with identifiable arthropods ($n = 12$). Only one faecal sample of Sedge Warbler collected in Paul da Madriz had identifiable remains and it contained Hymenoptera.

Table XV - Percentage of occurrence of each order of arthropods in the faecal samples of Sedge Warbler *Acrocephalus schoenobaenus* collected in Paul do Taipal.

	2011	2012	
	August	March/April	July/August/September
n	2	4	6
Araneae	-	-	16,67
Coleoptera	100	-	83,33
Diptera	-	50	16,67
Hemiptera*	50	-	16,67
Aphids	-	-	33,33
Hymenoptera	50	50	66,67
Psocoptera	-	25	16,67
Other**	100	100	100

*except aphids

**pieces too worn out to identify

3.3.2 Diet selectivity

Ivlev Indices (E) for Paul do Taipal and Paul da Madriz (Tables XVI and XVII) show that Reed Warbler has a preference for Coleoptera and Hymenoptera, as evidenced already by Tables XIII and XIV. Hemiptera were ingested in Paul do Taipal and highly preferred in Paul da Madriz as well as Diptera. The other arthropod orders were either avoided or not ingested at all, because the value of E was very close or equal to -1 (Tables XVI and XVII).

Table XVI - Ivlev's Electivity Index (E) for Reed Warbler *Acrocephalus scirpaceus* in Paul do Taipal. Only the most representative arthropod orders are shown here.

	Araneae	Coleoptera	Diptera	Hemiptera*	Aphids	Hymenoptera
March	-0.6	1	-	-	-	1
April	-0.62	-0.55	0.12	-1	-	1
May	-1	-	-1	-	-1	-
June	-0.78	1	-1	-	-0.92	1
July	-0.69	0.49	-0.24	1	-1	0.9
August	-0.43	0.94	0.3	0.67	-0.98	1
September	-0.14	0.85	0.54	1	-1	0.24
October	0.14	0.51	-0.64	-	-	0.37

*except aphids

Table XVII - Ivlev's Electivity Index (E) for Reed Warbler *Acrocephalus scirpaceus* in Paul da Madriz. Only the most representative arthropod orders are shown here.

	Araneae	Coleoptera	Diptera	Hemiptera*	Aphids	Hymenoptera
March	-1	-	1	-	-	1
April	-0.2	0	-	1	-	-0.43
May	-	-	-1	-	-1	-1
June	-1	1	1	1	-1	1
July	1	1	1	1	-	1
August	-1	0.99	-1	1	-1	0.97
September	-0.84	1	1	1	-	-0.38
October	-0.85	0.4	1	-	-	0.4

*except aphids

As for the Sedge Warbler, it appears to avoid practically every prey but Coleoptera during the autumn migration (Table XVIII). However, these results must be interpreted with great caution because the number of samples ($n = 12$) was very small.

Table XVIII - Ivlev's Electivity Index (E) for Sedge Warbler *Acrocephalus schoenobaenus* in Paul do Taipal. Only the most representative arthropod orders are shown here.

	Araneae	Coleoptera	Diptera	Hemiptera*	Aphids	Hymenoptera
March	-1	-	1	-	-	1
April	-1	-1	-0.04	-1	-	1
May	-	-	-	-	-	-
June	-	-	-	-	-	-
July	-1	0.69	-1	-	-0.01	-1
August	-0.51	0.75	-0.31	0.81	-0.9	1
September	-1	0.94	-1	-	-1	0.09
October	-	-	-	-	-	-

*except aphids

Table XIX - Comparison of presence of representative arthropod orders in Reed Warbler *Acrocephalus scirpaceus* faeces collected in Paul do Taipal and Paul da Madriz using a Chi-square test.

Araneae	$X^2_{(1)} = 0.12; p = 0.89$
Coleoptera	$X^2_{(1)} = 9.85; p < 0.01$
Diptera	$X^2_{(1)} = 4.44; p = 0.35$
Hymenoptera	$X^2_{(1)} = 3.18; p = 0.07$
Aphids	$X^2_{(1)} = 0.12; p = 0.72$

Only Coleoptera showed significant differences concerning presence in faecal samples of Reed Warbler of both study sites ($p < 0.01$) (Table XIX).

Chapter 4

Discussion & Conclusion

4.1 - Limitations of this study

Despite the effort to collect representative data in order to obtain significant results, that was not always possible. This work presents shortcomings due to the nature of the study species and some of the methodologies used. As stated in the literature (e.g. Bibby & Green, 1981; Bayly, 2007), Sedge Warblers make a single very long flight from southern England or northern France to sub-Saharan Africa by fuelling extensively on aphids. Hence, the expected number of Sedge Warblers captured in Portugal was low. This added to the fact that not all birds yielded a faecal sample and that roughly half of them contained unidentifiable arthropod pieces or nothing at all, contributes to explain the percentages of arthropod occurrence in the faecal samples and their influence in the results of the Ivlev Index for Sedge Warbler. Another caveat is the absence of arthropods counted in July in Paul da Madriz. Despite two countings in the period of that month, the absence seems unlikely given the peak of arthropod abundance in August. It is entirely possible that a different or complementary method could have obtained more realistic results.

4.2 - Migratory strategies

This study shows that Paul do Taipal is a much more extensively used habitat than Paul da Madriz by both Reed Warblers and Sedge Warblers, with significantly higher captures irrespective of age, seasons and years. The peak of passage of adults for both species in both sites was April for the Spring migration and end of July for the Autumn migration. As for juvenile Reed Warblers, the peak occurred in July and September in Paul do Taipal and Paul da Madriz, respectively, whereas juvenile Sedge

Warblers were not captured in Paul da Madriz and had two peaks of passage in Paul do Taipal. This pattern was to be expected from Reed Warblers since there is a breeding population in Portugal, which could lead to a lag between the passage of northern Europe populations and the departure of Portuguese breeders (personal data). This can be attributed, however, to the arrival of populations from north, although migration is an individual effort.

The average stopover duration of Reed Warblers during the spring migration was highly correlated with precipitation in Portugal and North Africa and wind speed in North Africa. Prevalence of rain and adverse winds often leads birds to wait for favourable weather to resume migration (Schaub, Liechti & Jenni, 2004; Bayly, 2007). Conversely, very high negative correlations with NAO and NAM values between December and March were found. A reduction in stopover duration is explained by the generally favourable weather conditions brought about by the reduced storminess and precipitation in the Mediterranean associated with a positive NAO and NAM index (Stenseth et al., 2003). A negative NAO index yields the opposite effect for stopover duration. Wind speed effect in Portugal was slightly adverse. As for average body weight variation, it was highly negatively correlated with precipitation in North Africa, since flight under rain carries additional energetic costs (Schaub, Liechti & Jenni, 2004). Positive correlations were found with NAO and NAM values between December and March. These parameters indicate that reduced precipitation and drier weather allow a more efficient feeding, since fattening rates are lower during rainfall due to reduced insect activity (Schaub & Jenni, 2001).

During the autumn migration, stopover duration was negatively correlated with NAO values between December and March and between August and October, NAM values between December and March and precipitation and wind speed in Central

Europe. As also stated for the spring migration, this can be related to more or less favourable conditions of departure associated with the value of the NAO and NAM indices. Strong tailwinds birds find during their migration reduce the time and energy spent to reach the next stopover site. Consequently, there is no need to refuel as much as it would without wind assistance. In addition, wind speed and precipitation in Portugal had a high positive correlation with stopover duration which might indicate adverse wind and weather. Body weight variation was highly positively correlated with wind speed in Portugal and had a negative correlation with NAO values between August and October, wind speed in Central Europe and monthly NAO values. This can be explained if birds face strong headwinds during a stopover. Faced with very adverse flying conditions, their choice might be continue to refuel until better conditions arise. Contrarily, absent adverse weather birds can also depart without refuelling. Since there is an associated cost when arriving at a stopover site for finding food (Hedenstrom & Alerstam, 1997), if birds depart without covering that cost they leave with lower energetic reserves.

In average, body condition values of Reed Warblers were negative during the spring migration and breeding season, and positive during the autumn migration. Birds arriving to Portugal coming from North Africa in the spring migration arrive underweighted after crossing an ecological barrier, the Mediterranean sea and perhaps, even the Sahara desert in the same bout. The breeding season is also energetically demanding, hence the lower body mass. During the autumn season, Reed Warblers arrive from England and Northern Europe still with fuel reserves previously accumulated. The same is true for Sedge Warblers but since they refuel more extensively than Reed Warblers and usually make direct flights from northern France until just south of the Sahara desert, they present greater body mass (Bibby & Green,

1981). Body condition is higher during the autumn spring than the spring migration in both Reed and Sedge Warblers. This can be tied to the fact that the distance covered from the last stopover site until Portugal is longer from sub-Saharan Africa than northern Europe.

From 2000 to 2012, there has been a trend of decreasing numbers of adult and juvenile Reed Warblers. Despite that, productivity has been rising almost uninterruptedly. This can be interpreted as a proxy for habitat quality. There are no significant differences between years and the population can maintain its stability.

Blood levels of metabolites varied significantly between Reed and Sedge Warblers and between spring and autumn migration. Triglycerides levels were significantly higher in Sedge Warblers than in Reed Warblers. This blood metabolite has been shown to reflect change in body mass (Jenni & Schwilch, 2001) and fat mobilization and, thus can be associated with different migratory strategies, according to its levels. The higher its levels in the blood stream, the greater the fat mobilization and the use of energetic reserves which translates in extended periods of flight without feeding. Lower triglycerides levels in Reed Warblers are indicative of shorter trips and, consequently, less accumulated energetic reserves.

Glucose blood levels were also significantly different between seasons. Glucose is the easily mobilizable, primary source of energy used and its concentration increases after feeding recently. Both species showed greater concentrations in the spring migration, which might be due to a depletion of reserves after arriving from North Africa and increase of glucose from feeding in order to be used immediately.

4.3 - Specialist vs Generalist diet

Although they are insectivore generalists, Reed Warblers seem to have a preference for certain arthropod orders. Ivlev's Index for Paul do Taipal shows that Reed Warblers actively seek Hymenoptera and Coleoptera from March until October, as the proportion found in faeces is greater than that found in the environment. Other orders, while appearing in the diet, are in much less numbers than in the environment, therefore their Ivlev Index values are lower. Although variable, the percentage of occurrence of Hymenoptera in Reed Warbler faeces remains high throughout the sampled months while there is general trend of increase of Coleoptera occurrence from spring until autumn. In Paul da Madriz, besides Coleoptera and Hymenoptera, Diptera and Hemiptera were also important food items. However, the percentage of occurrence was low during most of the months for Diptera and Hemiptera, as opposed to Coleoptera and Hymenoptera. This can possibly be attributed to the low number of faeces with identifiable remains which may skew the relative occurrence of each arthropod order found in the faecal samples. Also, the Ivlev Index can be highly influenced by the abundance of prey in the environment (Gras & Saint-Jean, 1982).

The number of faecal samples collected from Sedge Warblers was low, since this species is known for not refuelling extensively in Portugal (Bibby & Green, 1981) and collected only in Paul do Taipal. Ivlev's Index showed similar results to those of the Reed Warbler, with preference for Diptera and Hymenoptera during the spring migration and Coleoptera, Hemiptera and Hymenoptera during the autumn migration. It is interesting to note that aphids are actually avoided or not ingested instead of favoured in the Sedge Warbler. Again, this is most likely due to the low number of Sedge Warbler faecal samples.

Diptera was the only arthropod order showing significant differences between sites, with Paul do Taipal having greater abundance throughout all sampled months. All representative orders, apart from Coleoptera, showed significant differences between months with expected peaks of abundance in the summer. Aphid peak of abundance was in August, a result which is not that much different from that shown by Bibby & Green (1981). While similar to the peak of abundance of Sedge Warblers, there were no significant differences between the two variables. This, however, was not enough for Sedge Warblers to stay for prolonged periods of time refuelling.

4.4 - Conclusion

Despite their similar physiology and habitat, Reed and Sedge Warblers have very different migratory strategies. While Reed Warblers can be seen refuelling extensively, most likely in order to transverse the Mediterranean and possibly the Sahara desert, Sedge Warblers do not make long stopovers and have a general better body condition than Reed Warblers. In 12 years of ringing data, there were only 5 records of Sedge Warblers stopping to refuel in Portugal: twice in 2008 and 2009 and once in 2011, all in the autumn migration (stopover duration = 4.8 ± 1.92 , $n = 5$; body weight variation = 0.9 ± 1.4 , $n = 5$). This may be tied to the fact that Sedge Warblers arrive to Portugal after the peak of abundance of aphids, their favourite prey for refuelling. Even when present, they do not seem to give it preference over other food items when they stop in Paul do Taipal. Therefore, and in agreement with other studies published before (e. g. Bibby & Green, 1981) it can be assumed that Sedge Warblers, unlike Reed Warblers, do not refuel in Portugal.

Chapter 5

References

Åkesson S. & A. Hedenström (2000). Wind selectivity of migratory flight departures in birds. *Behavioral Ecology and Sociobiology* 47: 140-144

Åkesson S., Walinder G., Karlsson L. & S. Ehnbohm (2002). Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. *Journal of Avian Biology* 33: 349-357

Alerstam T., Hedenström A. & S. Åkesson (2003). Long-distance migration: evolution and determinants. *Oikos* 103: 247-260

Báldi A. & T. Kisbenedek (1999). Species-specific distribution of reed-nesting passerine birds across reed-bed edges: effects of spatial scale and edge type. *Acta Zoologica Academiae Scientiarum Hungaricae* 45: 97-114

Barnston A. G. & R. E. Livezey (1987). Classification, seasonality and persistence of low-frequency atmospheric circulation patterns. *Monthly Weather Review* 115: 1083-1126

Bayly, N. J. (2007). Extreme fattening by sedge warblers, *Acrocephalus schoenobaenus*, is not triggered by food availability alone. *Animal Behaviour* 74: 471-479

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

Bibby C. J. & R. E. Green (1983). Food and fattening of migrating warblers in some French marshlands. *Ringing and Migration* 4: 175-184

Chernetsov N. (2012). Passerine migration. Springer 13-14 pp

- Chernetsov N. & A. Manukyan (2000). Foraging strategy of the Sedge Warbler (*Acrocephalus schoenobaenus*) on migration. *Vogelwarte* 40: 189-197
- Cowardin L. M., Carter V., Golet F. C. & E. T. LaRoe (1979). Classification of wetlands and deepwater habitats of the United States. US Fish and Wildlife Service, 103 pp
- Cowie N. R., Sutherland W. J., Dithlogo M. K. M. & R. James (1992). The effects of conservation management of reed beds. II. The flora and litter disappearance. *Journal of Applied Ecology* 29: 277-284
- Cramp S. (1992). *The Birds of the Western Palearctic Vol. VI. Warblers*. Oxford University Press, Oxford
- Crawley M. J. (2007). *The R Book*. Imperial College London at Silwood Park, UK. ISBN-13: 978-0-470-51024-7
- Dingle H. (1996) *Migration: the biology of life on the move*. Oxford University Press, Inc. 23-25 pp
- Dithlogo M. K. M., James R., Lawrence B. R. & W. J. Sutherland (1992). The effects of conservation management of reed beds. I. The invertebrates. *Journal of Applied Ecology* 29: 265-276
- Eichelberger S. J. & J. R. Holton (2002). A mechanistic model of the northern annular mode. *Journal of Geophysical Research* 4388
- Gras R. & L. Saint-Jean (1982). Comments about Ivlev's electivity index. *Revue d'Hydrobiologie Tropicale* 5: 33-37

- Guglielmo C. G., Cerasale D. J. & D. Eldermire (2005). A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. *Physiological and Biochemical Zoology* 78: 116-125
- Gullan P. J. & P. S. Cranston (2004). *The insects: an outline of entomology*. Blackwell Publishing Ltd. 174 pp
- Hardman C. J., Harris D. B., Sears J. & N. Droy (2012). Habitat associations of invertebrates in reedbeds, with implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 813-826
- Hüppop O. & K. Hüppop (2003). North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London, B* 270: 233-240
- Jenni L. & S. Jenni-Eiermann (1998). Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology* 29: 521-528
- Jenni L. & M. Schaub (2003). Behavioural and physiological reactions to environmental variation in bird migration: a review. *Avian migration*, 155-171 pp
- Jenni L. & R. Schilch (2001). Plasma metabolite levels indicate change in body mass in reed warblers *Acrocephalus scirpaceus*. *Avian Science* 1: 55-65
- Karlsson H., Nilsson C., Bäckman J. & T. Alerstam (2011). Nocturnal passerine migration without tailwind assistance. *Ibis* 153: 485-493
- Kern J. & C. Idler (1999). Treatment of domestic and agricultural wastewater by reed bed systems. *Ecological Engineering* 12: 13-25
- Marra P. P., Francis C. M., Mulvihill R. S. & F. R. Moore (2005). The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142: 307-315

Martínez-Vilalta J., Bertolero A., Bigas D., Paquet J. Y. & A. Martínez-Vilalta (2002).

Habitat selection of passerine birds nesting in the Ebro Delta reedbeds (NE Spain):
management implications. *Wetlands* 22: 318-325

Minias P., Kaczmarek K., Włodarczyk R. & T. Janiszewski (2013). Hemoglobin
concentrations in waders vary with their strategies of migration: a comparative analysis.
Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology
165: 7-12

Mitsch W. J. & J. G. Gosselink (2007). *Wetlands* 4th ed. Wiley, John & Sons, Inc.

Ostendorp W. (1993). Reed bed characteristics and significance of reeds in landscape
ecology. *Limnologie aktuell* 5: 149-161

Ottersen G., Planque B., Belgrano A., Post E., Reid P. C. & N. C. Stenseth (2001).

Ecological effects of the North Atlantic Oscillation. *Oecologia* 128: 1-14

Péron G., Henry P. Y., Provost P., Dehorter O. & R. Julliard (2007). Climate changes
and post-nuptial migration strategy by two reedbed passerines. *Climate Research* 35:
147-157

Poulin B. & G. Lefebvre (2002). Effect of winter cutting on the passerine breeding
assemblage in French Mediterranean reedbeds. *Biodiversity and Conservation* 11: 1567-
1581

Ramsar Convention Secretariat (2013). *The Ramsar Convention Manual: a guide to the
Convention on Wetlands (Ramsar, Iran, 1971)*, 6th ed. Ramsar Convention Secretariat,
Gland, Switzerland.

- Rguibi-Idrissi H., Julliard R. & F. Bairlein (2003). Variation in the stopover duration of Reed Warblers *Acrocephalus scirpaceus* in Morocco: effects of season, age and site. *Ibis* 145: 650-656
- Schaub M. & L. Jenni (2000). Fuel deposition of three passerine bird species along the migration route. *Oecologia* 122: 306-317
- Schaub M. & L. Jenni (2001). Variation of fuelling rates among sites, days and individuals in migrating passerine birds. *Functional Ecology* 15: 584-594
- Schaub M., Liechti F. & L. Jenni (2004). Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Animal Behaviour* 67: 229-237
- Schmidt M. H., Lefebvre G., Poulin B. & T. Tschardtke (2005). Reed cutting affects arthropod communities, potentially reducing food for passerine birds. *Biological Conservation* 121: 157-166
- Stenseth N. C., Ottersen G., Hurrell J. W., Mysterud A., Lima M., Chan K. S., Yoccoz N. G. & B. Ådlandsvik (2003). Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London, B* 270: 2087-2096
- Strauss R. E. (1979). Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* 108: 344-352
- Svensson L. (1992). Identification guide to European passerines. Naturhistoriska Riksmuseet, Stockholm

Tansley A. G. (1935). The use and abuse of vegetational concepts and terms. *Ecology* 16: 284-307

Trnka A. & P. Prokop (2006). Reedbed structure and habitat preference of reed passerines during the post-breeding period. *Biologia* 61: 225-230

Yohannes E., Biebach H., Nikolaus G. & D. J. Pearson (2009). Passerine migration strategies and body mass variation along geographic sectors across East Africa, the Middle East and the Arabian Peninsula. *Journal of Ornithology* 150: 369-381

Yoon C. (2009). Wise use of paddy rice fields to partially compensate for the loss of natural wetlands. *Paddy and Water Environment* 7: 357-366

IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1.

<www.iucnredlist.org>. Downloaded on 1 July 2013.