AUTUMN MIGRATION DYNAMICS, BODY MASS, FAT LOAD AND STOPOVER BEHAVIOUR OF WILLOW WARBLER (*Phylloscopus trochilus,* Linnaeus 1758) AT MANYAS KUŞCENNETİ NATIONAL PARK (NORTHWESTERN TURKEY)

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ABSTRACT

AUTUMN MIGRATION DYNAMICS, BODY MASS, FAT LOAD AND STOPOVER BEHAVIOUR OF WILLOW WARBLER (*Phylloscopus trochilus* Linnaeus 1758) AT MANYAS KUŞCENNETİ NATIONAL PARK (NORTHWEST TURKEY)

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Turkey lies on one of major migratory routes between Palearctic and Afrotropical regions. Despite its importance for many species, few studies exist on bird migration over Turkey. In this study, autumn migration dynamics and stopover behaviour of Willow Warbler (*Phylloscopus trochilus*), a small insectivorous passerine, was documented and analyzed at Manyas Kuşcenneti National Park (northwestern Turkey).

Birds were mistnetted, ringed, measured, weighed and fat-scored from mid August in 2002 and end of August in 2003 to end of October in both years. Totally 543 and 929 Willow Warblers were ringed in 2002 and 2003 respectively.

For 2002 and 2003 respectively, fat score values (mean±SE) are 4.63±0.06 and 3.84±0.05 and body mass values are 11.38±0.07 and 10.37±0.05 grams for birds captured the first time. Fat scores in 2003 show a bimodal distribution with peaks of T2 and T5, indicating populations or age classes with different migratory strategies.

The number of retraps constituted 9.2-12.1 % of the total in 2002 and 2003. In both years, minimum stopover length ranged from 1 to 15 or 16 days with a median of 5 days. The majority of the retraps put on significant fat in both years. Retraps continued to put on weight for up to two weeks after they arrived.

In this first ever study documenting passerine migration at Manyas Kuşcenneti National Park, it was revealed that such wetlands provide crucial stopover habitat for many migrant passerines, enables them to gain necessary fat loads before crossing two ecological barriers, the Mediterranean Sea and the Sahara.

Keywords: *Phylloscopus trochilus*, migration, stopover behaviour, fat load, Manyas Kuşcenneti

ÖZ

MANYAS KUŞCENNETİ MİLLİ PARKI'NDA (KUZEYBATI ANADOLU) SÖĞÜT BÜLBÜLÜ'NÜN (*Phylloscopus trochilus* Linnaeus 1758) SONBAHAR GÖÇ DİNAMİĞİ, AĞIRLIĞI, YAĞ YÜKÜ VE KONAKLAMA DAVRANIŞI

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Türkiye Palearktik ve Afrotropikal bölgeler arasındaki ana göç yollarından biri üzerinde yer alır. Birçok tür için önemine rağmen Türkiye'de kuş göçü üzerine az sayıda araştırma yapılmıştır. Bu çalışmada, böcekçil küçük bir ötücü olan Söğüt Bülbülü'nün (*Phylloscopus trochilus*) Manyas Kuşcenneti Milli Parkındaki sonbahar göçü dinamikleri ve konaklama davranışı belgelenmiş ve analiz edilmiştir.

2002 yılında Ağustos ortasında, 2003 yılında Ağustos sonunda başlayan ve her iki yıl Ekim sonuna kadar süren çalışmada kuşlar sis ağlarıyla yakalanmış, halkalanmış, ölçülmüş, tartılmış ve yağ dereceleri belirlenmiştir. 2002 yılında 543, 2003 yılında ise 929 Söğüt Bülbülü halkalanmıştır.

2002 ve 2003 yıllarında kuşlardan ilk yakalandıklarında alınan yağ dereceleri ve ağırlık değerleri sırasıyla 4,63±0,06 ve 3,84±0,05 (ortalama±SH) ve 11,38±0,07 ve 10,37±0,05'dir. 2003 yılına ait yağ dereceleri T2 ve T5 kuşlarının zirve değerlerinden oluşan bimodal bir dağılım göstermekte ve farklı göç stratejilerine sahip populasyonların ya da yaş gruplarının varlığına işaret etmektedir.

2002 ve 2003 yıllarında sırasıyla kuşların % 9.2’si ve % 12.1’i tekrar yakalanmıştır. Her iki yılda da kalış süresi medyanı 5 gündür ve en kısa konaklama süresi 1 ila 15 veya 16 gün arasında değişir. Tekrar yakalanan kuşların büyük bölümü belirgin bir şekilde yağlanmış ve iki haftalık bir konaklama süresine dek ağırlık kazanmaya devam etmişlerdir.

Manyas Kuşcenneti Milli Parkında ötücü göçünü belgeleyen bu ilk çalışma, bu tip sulakalanların birçok göçmen ötücü kuş türü için Akdeniz ve Sahra Çölü gibi iki önemli ekolojik engeli geçmeden önce gerekli yağ yüklerini depolamaları için çok önemli bir konaklama alanı olduğunu ortaya çıkarmıştır.

Anahtar kelimeler: *Phylloscopus trochilus*, göç, konaklama davranışı, yağ yükü, Manyas Kuşcenneti

To Jno

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I have ringed my first bird in Sweden! I am grateful to all my friends in Kvismaren Bird Station, especially Åshild Jarnkvist for the invaluable experience and learning atmosphere.

Willow Warblers! Looking at your size first time in hand, I was amazed how you manage the journey of yours. Now I'm amazed even more, isn't it a good motivation to keep working?

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INTRODUCTION

1.1 General features of migration

The environmental conditions on Earth are not stable. In order to maximise fitness in these changing conditions, all living organisms must respond to such changes by adjustments in their morphology, physiology and behaviour. The challenges that living organisms face falls in three major categories: predictable changes (e.g seasonal changes which are also coupled with changes in resources), unpredictable changes (e.g. human effect), and changes in social interrelationships (Ramenofsky and Wingfield 2007).

Diurnal and annual periodicity, both of which are caused by earth's rotation around its axis and seasonally changing altitude of the sun's position are predictable changes that result in daily and seasonal patterns which greatly influence life cycle of all living organisms and to which they must respond in order to survive and reproduce. Migration is one of the responses to this periodicity and it is a widespread phenomenon observed in almost all groups of living organisms (Berthold 1993).

Migration is believed to have evolved independently among many groups of animals such as fish, mammals (including bats and marine mammals), insects, reptiles, marine invertabrates, amphibians and birds. Migration is in most cases primarily an adaptation for exploiting seasonal peaks of resource abundance and avoiding seasonal resource declines (Alerstam *et al.* 2003).

Since it is a common phenomenon in nature, the definitions of migration are also diverse. An early definition was given by Baker (1978) who described migration as "the act of moving from one spatial unit to another". Baker's definition is a very general one that fails to exclude some nonmigratory movements. A more refined definition by Webster *et al.* (2002) describes migration as "The regular seasonal movement of individuals, often from a breeding location to a nonbreeding location and back".

The forms of migration may vary from the simplest vertical movements between geographical units as a response to daily or seasonal changes affecting food resources and/or living conditions (e.g shelter from predators) to seasonal long-distance migrations of many animals from whales to desert locusts (Berthold 1993).

The migration patterns of birds are the most conspicuous, diverse and complex compared with all other taxa (Berthold 1993). There are more than 9000 species of birds currently inhabiting the Earth, several thousand of which show migratory movements. Birds have adapted to live very diverse habitats and they utilise almost all available habitats throughout their migratory journey (Berthold 1988).

Every autumn several billion land birds of approximately 200 species leave their Paleartic breeding grounds and migrate to Africa (Salewski and Jones 2006). The migration of birds have ignited much attention and curiosity of humans since the earliest times and been recognized as one of the most fascinating biological phenomena (Allard 1928, Moreau 1952).

1.2 The evolution of bird migration

It is believed that bird migration exists since the first birds inhabited the Earth, more than 100 million years ago, but the migration patterns of birds observed today have evolutionary histories of less than 10,000, and in most cases not more than 5000, years due to unstable environmental conditions. The contemporary migrants are largely products of the ice ages of the Quaternary epoch (Alerstam 1990).

There have been several important theories about the evolution of bird migration. Cox (1968) suggested intraspecific and interspecific competition as primary selective agents in the evolution of migration. Alerstam and Enckell (1979) argued that unpredictibility of the habitat would almost remove the advantages of prior occupancy by residents, and thus favour evolution of migration.

One of the challenging questions for evolution of bird migration is “Why some birds migrate and others don’t?” As the question implies, for the theory of evolution of migration, understanding of the non-breeding interactions between migrants and residents are also of utmost importance. The coexistence of migrant and resident conspecifics in nonbreeding areas continue to puzzle the scientists (Pérez-Tris and Telleria 2002) since residents may be better competitors against arriving migrant conspecifics. This shows that non-breeding processes may be as important as breeding benefits for the migrants in the evolution of migration.

Natural selection continues to mold and refine migration strategies of birds. Such strategies do not merely consist of stereotyped behavious but also there is great flexibility in behaviour, which is essential if the birds must be able to successfully meet the changing and unexpected situations that constantly come up during migration flights (Alerstam 1990).

The continuous evolution of the migratory patterns can be both natural and human induced. The long term climatic changes for example are known to affect the distribution and migratory habits of birds (degree of partial migration or distance covered) which are already observed in several species (Busse 1987, Berthold 1993).

Migratory behaviour may develop anew in previously non-migratory species or change in direction or timing in migratory populations even in modern times (Farner 1955). A most recent example is the increasing numbers of Central European Blackcaps (*Syliva atricapilla*) wintering in southern England instead of southern Europe or north Africa. These birds have increased over several decades from a few individuals to an increasingly behaviorally (and genetically) isolated population with different migratory routes and timing (Bearhop *et al.* 2005).

1.3 Genetics of migration

Migration has a significant genetic component that determines 1) the timing and duration of movement in the temporal/circannual program of the organism, 2) physiological adaptations for fuel deposition and metabolism, 3) behavioural adaptations for responding to the variable conditions (weather, wind, currents) during the journey and 4) control of orientation and navigation (Berthold 2001).

1.4 The variation of bird migration

Owing to thousands of bird species showing migratory movements and the wide distribution of these migratory systems, there is a high variety of bird migration patterns (Berthold 2003). The variation could be seen among species, populations, age groups and sexes. Further, it can also vary between years within individuals. The differences arise from the difference in distances covered by migrants, the migratory route followed, the timing of departure and arrival and the behaviour expressed during the migratory journey (Bairlein and Coppack 2006).

The most prominent migratory movement of birds is from northernly breeding grounds to southernly nonbreeding quarters and back. Other than this birds exhibit several more types of migratory pattern including intratropical migration, vertical migration and moult migration. Birds also show less migratory patterns such as irruption, invasion etc. (Berthold 2003).

1.4.1 Differential migration

The findings of some research (e.g Ketterson and Nolan 1976) revealed that many migratory populations exhibit differential migration, with differences of timing and migration distance between individuals (usually sex or age classes).

For example, first-year birds may migrate along different routes or may have different wintering grounds. Comparatively little is known about migration patterns, routes or destinations in different sexes in passerines although there is some evidence that they can differ (Bairlein 2001).

The most prevalent migratory movement of birds is believed to be obligate partial migration which could be defined as the case in which a fraction of the population migrates some distance annually while the remaining population stays on breeding grounds (Pulido *et al*. 1996). Obligate partial migration is considered as a transitional stage during the evolution of obligate migration (Alerstam and Hedenström 1998).

1.4.2 Long-distance migration

Although many bird species show simple form of migrations such as seasonal vertical migrations or short-distance migrations, some are capable of long–distance migrations where even distances equivalent to the Earth’s circumference are covered (Berthold 1993). Birds hold the record for long distance migration with Arctic tern (*Sterna paradisaea*) covering nearly 20,000 km in a one way trip from high artic to survival and moult areas in the Antarctic peak ice zone (Salomonsen 1967).

In birds, long-distance from a zoogeographical point of view means that the breeding and wintering range of the species are seperated by areas where the species only is observed on passage. It is commonly observed in European passerines with 63 species, 49 and 14 of which are African and Asian migrants respectively (Busse 1987).

According to Lack (1968), the main adaptations needed for long-distance migration are fuel load, timing mechanisms and the ability to orientate.

1.4.3 Adaptations for long-distance migration

The advantage of migration for birds is that it allows for year-round activity unlike dormancy or hibernation, and thus they can exploit the effects of seasonality (suitable habitats and resources). On the other hand, the demands of migration are potentially great. In order to cope with these high demands, migratory birds are equipped with specific adaptations which involve morphology and physiology for efficient energy accumulation and locomotion, and behavioural adaptations for external factors (winds, currents, orientation cues) (Åkesson and Hedenström 2007). An example to morphological adaptations would be the longer and more pointed flight feathers of long–distance migrant populations than their short-distance migrating cousins.

The complex behavioral and physiological state of a migrant which has prepared itself for migration is coined with the term “migratory disposition”. During this state, birds change their feeding habits and metabolism. Before the start of the migration period migrants suddenly and spontaneously start eating large quantities of food (a phase called hyperphagia). Consequently extensive fat reserves are accumulated by migrants which is the main characteristics of migratory disposition (Berthold 1993). The observation of hyperphagia in caged birds belonging to migrant populations shows that this process is controlled by an endogenous, inherited program that bases on the internal biological clock (Ścisłowska and Busse 2005).

Migratory birds need these stored fat reserves for their migratory journey as flight fuel. The lipids are the most energetic molecules that could be stored in the birdy body. Energy amounting to around 9 kilocalories is released when 1 g of fat is burned. Only less than half of this value could be obtained from carbohydrates or proteins. Another advantage of storing fat in migrant body is that it does not require extra water for storage. Therefore, fat is optimal flight fuel for migrants whose target during migration is to put on as much energy-light fuel as possible without becoming too heavy (Ścisłowska and Busse 2005, Alerstam 1990).

The stored fat may be distributed throughout different parts of the migrants body but as much as up to half of the total stored fat can be found just under the skin, and hence visible in apteria. The visible fat reserves of a bird are deposed in furculum, on the belly and sides, from where they can cover even the breast muscles. The rest of the fat is invisible, being located inside of the body or under pterylae (Busse 1970, Ścisłowska and Busse 2005).

The amount of fat reserves is related to the migratory distance to be covered and associated ecological conditions, the stages of migration, body size and the systematic group that a particular migratory bird belongs to. Passerines that are non-migratory show fat stores of only 3-5% of their lean body mass whereas long-distance passerines are known to reach at departure, fat loads around 30-50% of their live body mass (60-100% of fat-free body mass). This means that the migrants double and even slightly more than double their body mass. On the other hand, the average fat loads of short to medium distance migrants is only in the range of 10-25% of body mass (Berthold 1993).

The process of fattening prior to departure and utilising fat reserves during active passage is a very dynamic one. Although during one continous flight migrants can loose as much as 30% of their body mass at start, they can daily gain as much as 10% of their fat-free body mass. The mean fat load during any of the migratory stage is thought to be more or less stabilised (Ścisłowska and Busse 2005).

The capacity of flight muscles and costs of flight transport are factors of utmost importance that can limit the amount of fat that could be stored by a migrant. The increase in fat stores lead to an increased overall weight which in turn cause greater resistance of air (drag). There is a limit to the capacity of flight muscles undertaking powered flight with these loads. In order to cope with this heightened demand of flight, migratory birds strengthen their flight muscles before migration. This phenomenon is called muscle accretion and observed in small passerines like Willow Warbler with approximately 1 g. increase in muscle mass (Alerstam 1990).

The transport economy of high fat loads is poor. A bird which stores up to 50% of fat and flies until the reserves are fully depleted actually consumes approximately 40% more energy than a bird which would start by building up only 10% fat reserves and fly till its reserves are finished, stop and build up 10% fat store again and repeat this process 6-7 times covering totally the same distance as the first bird (Alerstam 1990).

However, birds cannot apply this more economic flight method in all circumstances. There are ecological barriers like oceans, glaciers, deserts where birds cannot stop and replenish their fat reserves. Instead before such barriers, birds are compelled to accumulate as much fat stores as possible for a safe flight (Alerstam 1990).

1.5 Ecological barriers

Deserts, oceans, high mountain ranges that constitute ecological barriers are considered to have great evolutionary significance for migratory birds with effects varying between birds and migratory systems (Moreau 1972, Henningsson and Alerstam 2005) Alerstam *et al.* (2003) lists the three main consequences of such barriers as: 1) They may simply put a stop to further migration; 2) They may lead to evolution of detours, where the crossing of barriers is avoided or reduced; and 3) Long-distance crossing of barriers requires that special instructions are incorporated into the migrants' endogenous spatiotemporal circannual programme (Gwinner 1996, Berthold 2001) about increased fuel deposition and sometimes changes in the orientation (Gwinner and Wiltschko 1978) at the barrier.

The crossing of ecological barriers often involves risks of starvation, disorientation, drift and predation (Alerstam 2001). The strategies of migrants to overcome barriers depend both on the type of the barrier and on the prerequisites of different migratory bird populations. In general the strategy of migrants to cross barriers is attaining maximum fat reserves which provides them with safety during unpredictable delays and as well equip them with a higher flight speed and as a result a swifter passage over the barriers (Berthold 1993).

1.5.1 Autumn barriers for European - African migrants: Mediterranean Sea and the Sahara

Migratory birds within the European–African migration system face two ecological barriers, the Mediterranean Sea and the Sahara, both of which offer very few oppurtunities to replenish fat reserves (e.g. islands, oases) over large distances (Schaub and Jenni 2000).

Moreau (1961, 1972) postulated that Eurasian migrants heading for wintering grounds in Africa crossed both the Sahara and the Mediterrenean in an extensive non-stop flight of some 30-40 hours. Although fat reserves of many migrants would theoretically facilitate such a vast migratory step, many recent studies revealed that many migrants actually landed in the desert (Berthold 1993). Many birds from the southwestern and southeastern flyways are known to circumfly the Mediterranean Sea via the Iberian Peninsula or the Middle East. The Sahara however cannot be avoided and birds must be equipped with the necessary fat loads to carry them over around 2000 km of desert without refueling, but possibly with stopover (Bruderer and Liechti 1999).

According to their radar study results, Biebach *et al.* (2000) classify three groups according to different strategies of Mediterrenean and Sahara crossing: 1) The day group of birds that performs non-stop flight across the sea, and at least the northern part of the desert; 2) the night group that performs an intermittent flight strategy with stop over at the coast of Egypt to continue migration the next evening; and 3) the evening group which also shows intermittent flight, but which stops somewhere in the desert after a continous sea crossing and covering part of the desert. According to their observations, 20% of migrant individuals exhibited non-stop migration and 80% showed intermittent migration with a stopover at the coast (70 %) or desert (10%). The authors argue that any species of a small passerine has the option to use any of these three strategies.

1.6 Stopover ecology

Stopovers are crucially important for most small passerines since it is not possible to complete their intercontinental migration period without refuelling (Berthold 1975, Blem 1980). The typical migratory journey thus is made up of several flight periods where fat load is used as fuel to cover distances and stopover periods where birds cease the flight period at a stop and replenish their fat reserves to make next stages of flight. As a fact, birds are known to spend more time and energy on stopover than flight during the migration (Alerstam and Hedenström 1998, Schaub *et al.*2001). Fransson (1995) gives the ratio of time spent in active flight and stopover in autumn and spring for several warbler species as 1:7.

The stopover ecology of migrants is of utmost importance in describing and understanding bird migration systems although such studies are limited for most species. Of particular importance are studies at stopover sites within the range of a species where it occurs only as a passage migrant, since frequently the status changes are first noticed at the edge of the range (Lawton 1993). Suitable stopover sites before crossing the barrier are also of profound importance for the succes of migration but scarcely studied (Yosef and Chernetsov 2005).

The stopover duration and the fuel deposition rate are crucial factors shaping migration strategies of birds (Alerstam and Hedenström 1998). Therefore crucially important aspects to investigate at stopover sites are the estimation of duration of stop over and checking if any variation occurs between stopover behaviour for different groups of birds (Schaub *et al.* 2001).

The fuel deposition rate at stopovers largely determines the speed and success of migration. The analysis of fuel deposition rate along the migratory route and comparison of this parameter between stopover sites, seasons, days, age and sex groups, individuals gives clues to migration strategies adopted by different groups (Schaub and Jenni 2001).

1.7 Aims and scope of the study

This is the first systematic study on Willow Warblers in Turkey covering approximately two months of the species' autumn migration in two consecutive years.

The aims of this study are:

- To find out the autumn migration dynamics (phenologies) of Willow Warblers at Manyas Kuşcenneti National Park.
- To record and analyze changes in biometrics, body mass, fat load and stopover duration between years and between age and sex groups.
- To find out the importance of Manyas Kuşcenneti National Park as a stopover site

CHAPTER 2

MATERIAL AND METHODS

2.1 Study species

Willow Warbler (*Phylloscopus trochilus,* Linnaeus, 1758) is a small insectivorous passerine that belongs to the genera *Phylloscopus* (Leaf Warblers) of the family Sylviidae (Old World Warblers) within the order Passeriformes of the Class Aves (Cramp 1992, Mullarney *et al.* 1999). It is a small and neatly built warbler with thin legs and a pointed bill. It has a length of 10.5 –11.5 cm and a wingspan of 16.5-22.0 cm. It has usually a pale and bright plumage with yellow-white underparts and with upperparts essentially olive colored with grey and brown present differing with relation to the population. It has a moderately distict, pale yellowish-white supercilium and typically yellow-brown legs. The species feed on wide variety of small insects and spiders, including fruit and berries in autumn. Its song is a rich descending warble with a flourish at the end; its call is a disyllabic `hoo-eet' (Cramp 1992, Mullarney *et al.* 1999, Svensson 1992).

Figure 2.1 Willow Warbler

The Willow Warbler is known to breed in upland birch and willow zone, nearly in all types of woodland, gardens, parks and deciduous scrubs. In African wintering grounds shows a high degree of adaptation to a wide range of habitats including also disturbed and cultivated areas but not favoring evergreen forest and acacia steppe (Mullarney *et al.* 1999, Jonsson 1992, Cramp 1992). On migration it occurs in steppe woodlands, willow and tamarisk thickets, reedbeds by ponds and rivers, forests, parks and gardens (Cramp 1992, Kasparek and Bilgin 1996).

All of the populations of Willow Warbler are migratory. It commonly breeds at high densities throughout the Palaearctic from northern Europe to Northeastern Siberia and commonly winters in sub-Saharan Africa from southern Senegal east to Ethiopia, south to South Africa (Cramp 1992). It is a nocturnal, long distance migrant that has one-way distance records such as between Chukotka and South Africa mounting up to 15,500 km. (Alerstam *et al*. 2003).

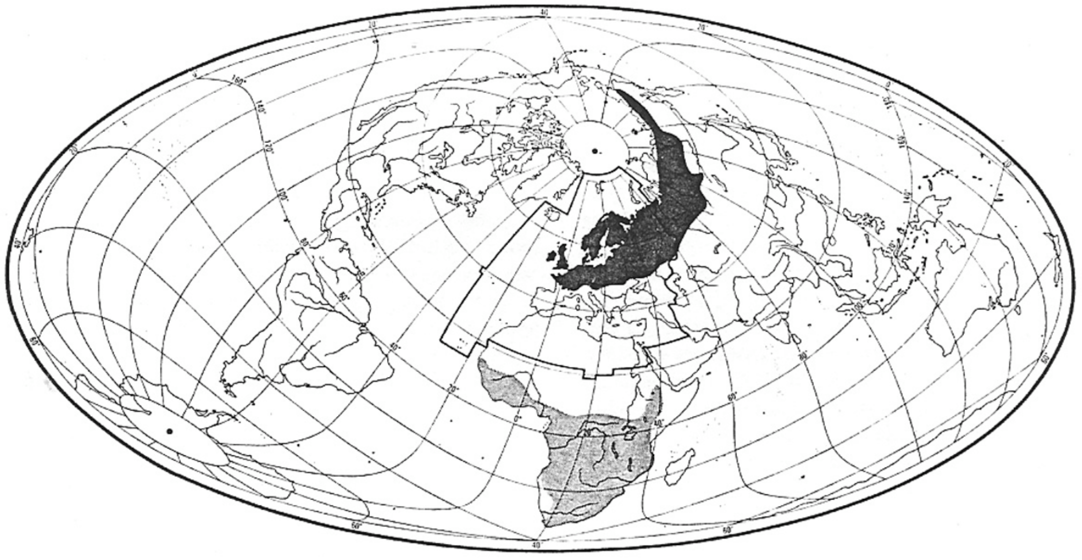

Figure 2.2 The distribution map of Willow Warbler. Black shows breeding grounds and gray shows wintering grounds (Cramp 1992).

The variation within the species is known to be slight and clinal with wide areas of intergradation making assigning of even populations to a certain subspecies difficult. Two races breed in Europe (*trochilus* and *acredula*) and a third (*yakutensis*) may occur as a vagrant in Western Europe (Svensson 1992).

In eastern Europe, the races *trochilus* and *acredula* are regular on passage through Greece (Bauer *et. al.* 1969). In Malta mostly nominate *trochilus* are recorded (Sultana and Gauci 1982) while in Crete it is mostly *acredula* (JR Parrott in Cramp 1992). In Cyprus, wing lengths average closest to nominate *trochilus* in the autumn and *acredula* in the spring (Flint and Stewart 1983) and both races are recorded in Eygpt (Goodman and Meininger 1989). Chamberlain *et. al* (2000) suggest that populations belonging to *acredula* as well as perhaps some eastern populations of *trochilus* migrate south-southeast.

In Turkey it is a common passage migrant during both spring and autumn migrations (Porter 1983, Keşaplı Can and Keşaplı Didrickson 2003, 2004). There is no evidence for the species breeding in Turkey but there are a few wintering records from the Aegean and Marmara regions (Kasparek and Bilgin 1996). It is known that different subspecies of Willow Warbler occur during passage in Turkey. These are the subspecies *trochilus*, *acredula, eversmanni* and *fitis* (Bilgin and Kasparek 1996). The latter two subspecies are often combined under *yakutensis* (e.g. Svensson 1992).

Another leaf warbler that could easily be confused with our study species is Chiffchaff (*P. collybita*). Chiffchaff is a short-distance migrant that could be told apart from Willow Warbler by clear emargination of 6th primary in hand and by its song in the field (Svensson 1992).

2.2 Study area

The study was carried out at Manyas Kuşcenneti National Park (40º 14' N 28º 02' E 16 m a.s.l.) which is situated by the northeast coast of Kuş (Manyas) Lake, (South of Marmara Sea) in northwest Turkey.

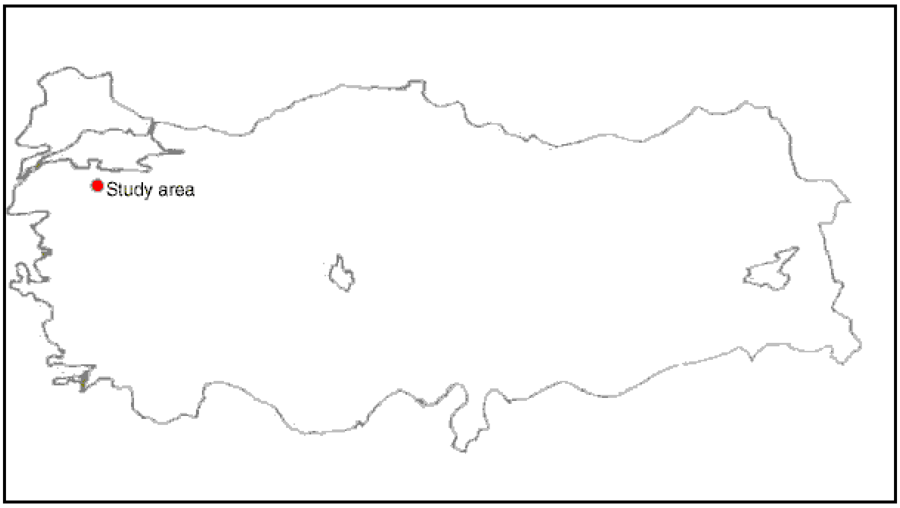

Figure 2.3 Study area on map of Turkey.

Kuş Lake (15,700 ha) is a shallow eutrophic freshwater lake with an average depth of 3 m. The lake's water is supplied both by the Kocasu (Madra), Sığırcı, Mürvetler and Dutlu streams and as well by the groundwater. Manyas Kuşcenneti National Park (64 ha) is located at the delta formed where Sığırcı stream enters the lake (Yarar and Magnin 1997).

The habitat of the National Park is dominated by seasonally flooded willow forest (*Salix alba, S.caprea* and *S. excelsa*) and dense reedbeds (*Phragmites australis, Typha angustifolia)* fringing the lake. Water lily *(Nymphaea alba)* and Sanicle-leaved Water Crowfoot (*Ranunculus saniculifolius*) can be found near or within the reedbeds. Besides willows, several other trees are present at the park area including ash-tree (*Fraxinus spp*). The delta where the park is situated also offers damp meadows and muddy flats depending on the season and precipitation (Karauz Er *et al*. 2007). The agricultural fields adjacent to the park also contibute to the richness of habitats for birds having different plantations each season. In the autumns during this study there were extensive sunflower (*Helianthus annuus*) plantations.

Figure 2.4 Views from the Manyas Kuşcenneti National Park substation

2.3 Methods

This study focuses on autumn migration data of Willow Warblers captured at Manyas Kuşcenneti National Park in the years 2002 and 2003. The data analysed in this study was collected during a larger scale ringing study carried out in 2 substations around the Kuş (Manyas) Lake, both in spring and autumn migration periods in 2002 and 2003 by Turkish Bird Research Society (KAD) with Southeastern European Bird Migration Network (SEEN) support in which the M.Sc. candidate worked at all seasons as head of the station.

Within the larger scale ringing, the spring migration studies were chiefly carried out at Soltra substation southeast of the national park and autumn ringing studies were mainly carried out at Manyas Kuşcenneti National Park substation. However in 2002 the autumn migration ringing study started at Soltra substation on 16th of August and continued at Soltra substation until 12th of September when the substation was finally closed due to very low migration activity.

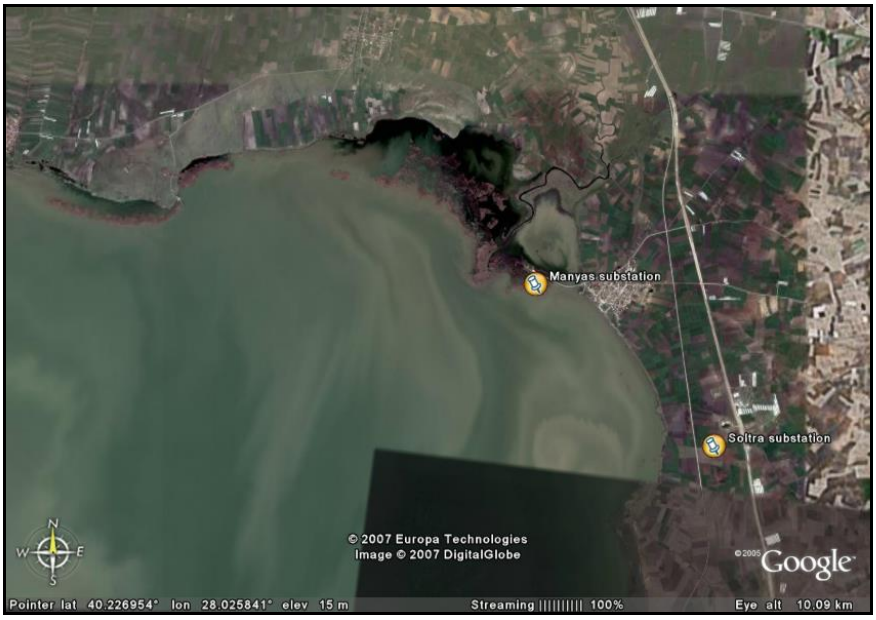

Figure 2.5 Positions of substations near Lake Kuş (Manyas)

Some opportunistic ringing had already been carried out at the park with a few nets whenever ringing at Soltra substation could not take place due to the weather conditions. Despite the few number of nets the catch at the park was promising. Thus the autumn ringing study was moved to Manyas Kuşcenneti National Park on 14th of September and continued until 22nd of October. The study was carried out during this period without a break for 38 days. The opportunistic ringing at the park however was carried out only for 6 days; 4 full days of work (25, 31 August and 1, 6 September) and 2 days from late morning (30 August and 5 September).

The autumn ringing in 2003 took place at Manyas Kuşcenneti National Park between 26th August and 19th October. The study was carried out continuously for 55 days. During this period the nets were open for 24 hours for a total of 42 days. Due to the weather conditions nets were closed for varying number of hours for a total of 11 days (26 and 31 August ; 4, 5, 11 and 12 September and 6, 7, 8, 10 and 19 October) and were closed for the whole day for a total of 2 days (29 August and 9 October).

Methodology was based on capturing, ringing and obtaining physiological and biometrical data of Willow Warblers. The misnetting and handling routine followed the guidelines of

SEEN. For catching 7 and 12 m long and 2m high mist nets with 4 shelves especially produced for passerine catching were used. The nets were made up of thick nylon thread with 16 mm mesh size (knot to knot).

Nets were placed mostly at the borders of different habitats (i.e between reeds and open water, bushes and trees etc) since they are known to be effective catching spots. Several other nets were also placed within the route according to the observed pattern of bird activity in the area. The nets were placed so as to make a short control loop to minimize the time spent during net checks. Net positions and net sizes were tried to be kept constant throughout the season but nevertheless replacement, addition and deletion of nets took place especially in 2002 since the ringing was carried out in the area for the first time.

Table 2.1 Effort spent in terms of net length per year in Manyas Kuşcenneti National Park

Study year - study period	Before mid-September	After mid-September
2002 (14/09-21/10)	209 m	371 m
2003 (26/08-19/10)	309 m	373 m

In Soltra substation between 16th of August and 12th of September 371 m of net was used but for a clearer picture of comparison between years the Table 2.1 shows only the effort. spent in the same locality; Manyas Kuşcenneti National Park substation.

The beginning and the end of the study period was tried to be determined according to previous records and literature data on passerine passage through the study area but especially the beginning of the migration period could not be ideal due to logistical problems.

Nets were open for the whole day following SEEN methodology (Busse 2000). The nets were controlled once at the beginning of every full clock hour. If there was some rain and/or wind or if the weather was too warm the nets were controlled more often. If the weather conditions were harsher the nets were closed. The first control was done either at or up to half an hour after sunrise. The last net control was done at complete dark, not later than 1.5

hour after the preceding check. The birds were freed from the nets gently and delivered to the ringing table in transpiring cotton bags.

When the ringed birds were captured again during the same migration period, they were called “retraps”. The ring number, date and hour of such captures was recorded in the logbooks. They were not fully processed again but their fat score and weight was remeasured to track changes from first capture. Retrapped birds provide important information in any ringing study. In this study we assume that if a bird is not retrapped again, it departed and continued its migration, rather than stayed longer although number of individuals can stay longer but they were not trapped by chance.

As a whole, the M.Sc. candidate was in the field for 55 days and did at least one third of the ringing in 2003. In 2002 although M.Sc candidate was present in appr. 75% of the ringing work, most ringing was carried out by SEEN ringers. At any time 1-4 helpers assisted with the work.

At the ringing table the birds were taken out of the bags and processed in an order. First, the species identification was done with the help of guide books; “Identification Guide to European Passerines” (Svensson 1992) and Collins Pocket Guide Birds of Britain & Europe with North Africa and the Middle East (Mullarney *et al.* 1999). The grip of the bird and the measurement techniques were adapted from “Bird Station Manual” (Busse 2000).

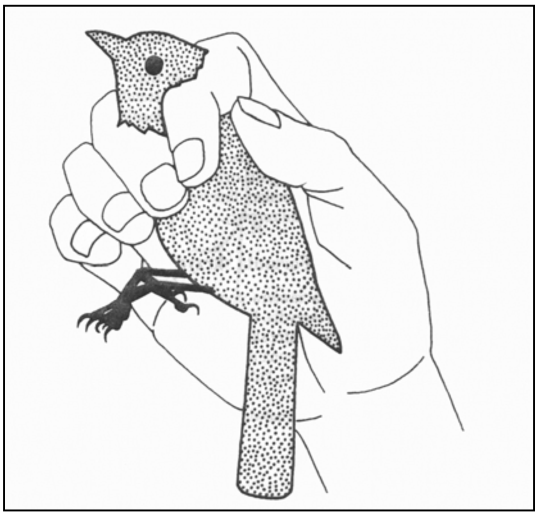

Figure 2.6 Standard ringers grip (Busse 2000)

The Willow Warbler is easily identified since when in the hand there are several straightforward characters that tells the species apart from the most similar species such as Chiffchaff *Phylloscopus collybita.* The most important of these characters is the emargination of 6th primary (Svensson 1992). After the species identification aluminium rings of 2mm diameter were fitted to the Willow Warblers left tarsus. These rings could be fitted by fingers without a need for pliers. The rings used in the study were national rings with the address ODTÜ KAD ANK TURKEY and a unique serial number allowing for individual identification of each bird.

Following ringing, Willow Warblers were aged according to the personal training from Prof. Busse, other visiting ringers and by the criteria given in “Identification Guide to European Passerines” (Svensson 1992) and “ Moult and ageing of European Passerines” (Jenni and Winkler 1994). Plumage characters and visual observation of skull ossification was used for age determination (See Appendix A for key for skull ossification). Immatures could often be told apart from adult birds with throat and breast yellow, rather strongly and more or less evenly coloured, not streaked yellow on white ground (Svensson 1992).

2.3.1 Sex determination

Although it is possible to sex some species of passerines according to plumage characteristics, this is not possible for Willow Warbler. Breeding individuals could be sexed reliably according to the incubation patch (Busse 1984, Svensson 1992). However, in this study only autumn passage birds that are not sexually active were captured so this method is not applicable.

It is known that Willow Warblers show sexual dimorphism with males being larger than females, and wing length could be used as a basis for sexing (Busse 1984, Tynjälä *et al.* 1993). Wings of males are on the average 4 mm larger than those of females (Cramp 1992). Generally in passerines the immature wings are shorter from adults (Busse 1984). In Willow Warbler this difference is given as 2 mm (Norman 1983). Therefore the sexing criteria for the captured Willow Warblers were determined separately for adults and immatures. As a result of the adoption of this sexing criteria, only aged birds were allocated to either sex.

The wing-length distribution of Willow Warblers was analysed separately for both age classes for both 2002 and 2003, and also for the total (Figures 2.7). In 2003 the sample size was bigger and the study was continous for a longer period at one locality, therefore the decision for wing-length threshold values were based largely on 2003 and total values. Based on the two discernible peaks in wing-length frequency graphs for adults and immatures and the available literature (Svensson 1992, Cramp 1992), the following sex allocation criteria was adopted: For immatures, birds with wing length equal to or smaller than 65 mm were designated as females and birds with wing length equal to or larger than 67 mm were designated as males. Any birds with a wing length of 66 mm were excluded from the analysis as these could be equally of either sex. For adult birds with wing length equal to or smaller than 67 mm were designated as females and birds with wing length equal to or larger than 69 mm were designated as males. Any birds with a wing length of 68 mm were excluded from the analysis.

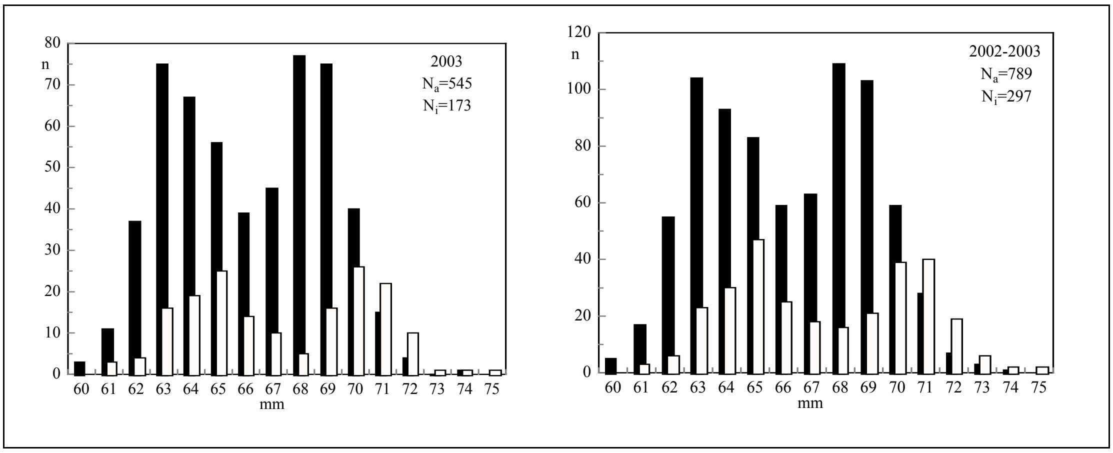

Figure 2.7 The distribution of the wing-length of immatures and adults in 2003 (left) and 2002-2003 (right).

2.3.2 Biometric measurements

Following aging the birds were fat-scored visually based on a 3 level - furculum, belly and pectoral muscles - inspection key according to a 9 (from 0 to 8) graded scale (after Busse 1983 and Kaiser 1993, combined. See Appendix B for key for fat determination). Later the wing length (maximum chord measurement Figure 2.8) of each bird were taken using a 30 cm long ruler (1 mm precision) cut off at point zero. The wing length was taken only if the longest primary feather was intact. The tail length was measured by "to the back" method (Busse 2000 Figure 2.9). The tail measurements were only taken if the longest tail feathers were in good condition. Finally the bird was weighed with an electronic scale to the precison of 0.1 g and immediately released afterwards.

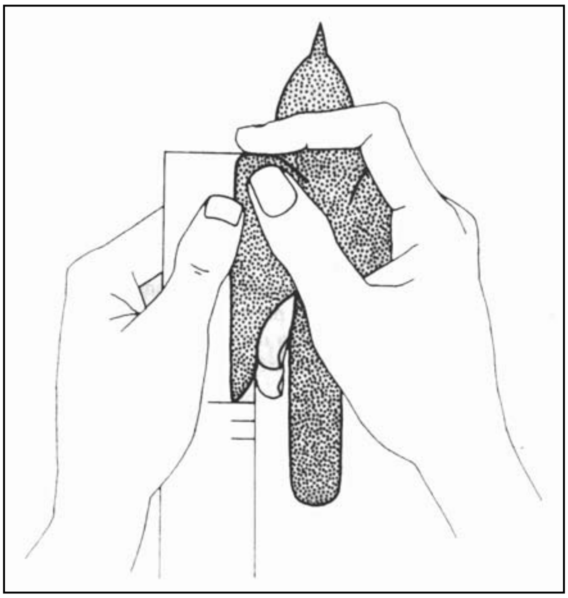

Figure 2.8 Wing length measurements (Busse 2000)

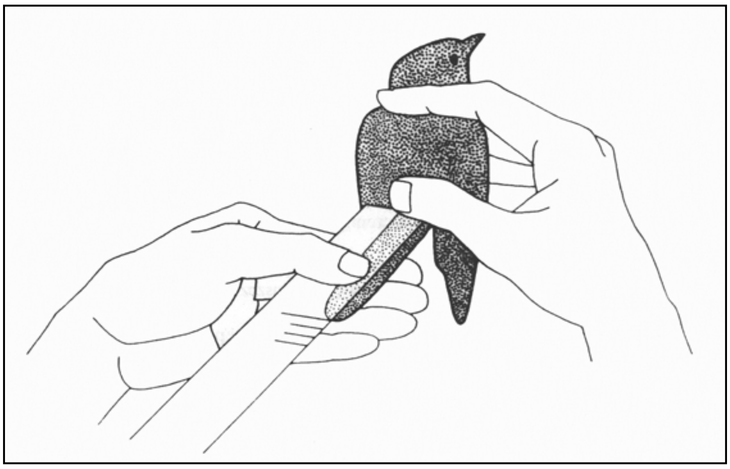

Figure 2.9 Tail measurement (Busse 2000).

Although the data collection routine is as above it is not always practically possible to take all measurements for each bird. The birds can have damaged feathers that makes biometrical data collection impossible, they can escape in the middle of the handling process, the ringer and/or the person who fill the data book could forget to collect some of the routine measurements. As a result of these circumstances in the field during data collection, the sample size for each of the characters analysed is different from the total number of measured birds.

2.4 Data analysis

Results were analyzed (including basic statistical tests) using custom built ringing analysis software PODAB (Version 7.0) as well as spreadsheet software Quattro Pro or Microsoft Excel.

In order to remove excessive variation within raw data, smoothing based on weighted running averages was used. Smoothing of data was carried out by repeating 5-day running average four times and using the formula:

$$D_x= 0.06*(d_x-2)+ 0.24*(d_x-1)+0.40*(d_x) +0.24*(d_x +1)+0.06*(d_x+2)$$

where d_x is the number of birds ringed on the xth day (Busse, 2000).

Weight and fat score are important parameters used in evaluation of a bird's condition. Although they are closely related there isn't a linear relationship between these parameters. Therefore, they should be treated separately as birds of equal weight may have very different fat content, and hence, lean body mass. Lean body mass is the weight of a relatively fat free bird. There may be some remnants of fat in the bird which are usually not readily available as a fuel but the bird is not in a starving condition (Busse 2000).

Fat reserves are individually and locally very variable, and since they are a part of the whole body mass, they greatly influence measurement of the weight. The stage of migration also has an influence as the same group of birds at different stages of migration will have different body mass due to different fat levels. These indicate that using the body mass parameter alone in order to characterise the average size of birds in population without taking into consideration the results of fat score would lead to a misinterpretation (Ścisłowska and Busse 2005).

In order to compare body mass of group of birds without them being masked by fat load and without killing and dissecting them to extract fat for a precise weight of fat load and lean body mass, a method was developed by Busse (1970) where the weight was standardised.

Standardised weight is a calculation based on average actual body mass for each fat score obtained in the field. The differences of each average is then used as a correction to adjust each bird to a particular fat class, in this case fat class 2. As a result, the standardised weight of each bird in the sample is calculated as the weight that the bird would have if it would have a fat score of T2. PODAB automatically calculates fat load in grams based on standard weight, using the formula

$$(\sum n_i * c_i) / N = t_g$$

where n_i is the number of individuals, c_i is the correction for a particular fat class, N is the total number of the group and t_g is the fat in grams for that group.

CHAPTER 3

RESULTS

3.1 Capture statistics

The total numbers of ringed Willow Warblers were 543 and 929 for years 2002 and 2003, respectively. There was 1 individual in 2002 and 6 individuals in 2003 that were found dead in the net. Although these birds were not ringed all possible biometrical data were collected. There were 50 and 112 individuals that were retrapped during 2002 and 2003 respectively. In 2002, between 16th of August and 12th of September ringing was carried out in Soltra substation and on 14th of September the study was moved to the Manyas Kuşcenneti National Park due to low autumn migration activity of passerines in general (only 26 Willow Warblers were captured in this period) (Table 3.1).

Table 3.1 Number of birds ringed and retrapped in 2002 and 2003.

Study period	Ringed	Measured*	Retrapped	% retrapped
2002 (16/08 - 21/10)	543**	544	50	9.21
2003 (26/08 - 19/10)	929	935	112	12.06
Total	1472	1479	163	11.07
* Including dead individuals that were not ringed but measured. **26 birds were caught at Soltra substation between 16th August to 12th of September.				

It is usually not possible to age all the birds during ringing studies. Only 68.01% and 77.65% of all captured birds could be aged in 2002 and 2003 respectively. The number of adults and immatures are 124 and 246 for 2002 and 178 and 548 for 2003 respectively. According to the simplified method of sexing (See 2.3.1 for details) only 61.95% and 72.19% of the aged birds could be allocated to either sex in 2002 and 2003 respectively. In 2002, the numbers of females and males are 169 and 168 respectively. In 2003, the same numbers are 340 and 335, respectively. For both years the sex ratio is roughly 1.0.

3.2 Seasonal dynamics of migration

3.2.1 Overall pattern of migration

Both in 2002 and 2003, the first Willow Warbler was caught immediately at the very first day of field work; on 16th and 26th of August respectively. In 2002 the migration peaked on 27th September with 56 individuals caught. The peak of migration corresponded to exactly the same date in 2003 with 58 individuals being caught (Table 3.2).

The last Willow Warbler was ringed on 18th and 19th of October in 2002 and 2003 respectively, but the latest captured bird during the whole study period was a retrapped individual on 20th of October in 2002.

As for age specific differences, the median dates of adults and immatures are different by 5 days in 2002. In 2003, the median days of passage for age groups are the same (Table 3.2).

Table 3.2 Dates of Willow Warbler migration in autumn 2002 and 2003.

	The earliest	The latest	Peak	Median
2002 (all)	16 August	18 October	27 September	30 September
Adult	23 August	16 October	2 October	3 October
Immature	16 August	16 October	27 September	28 September
2003 (all)	26 August	19 October	27 September	21 September
Adult	26 August	17 October	17 September	21 September
Immature	30 August	19 October	27 September	21 September

Figure 3.1 shows the smoothed total phenologies for the years 2002 and 2003. The phenology graph for 2002 covers the whole study period including data from Soltra substation. The dotted line marks the time period when the ringing study in 2002 was moved to Manyas Kuşcenneti National Park after which the locality and effort spent in terms of net length enable full comparison of migration dynamics between years.

The general phenology graph for 2002 reveals a single obvious peak towards the end of the season whereas in 2003, three peaks are discernible. The first peak in 2003 is smaller but covering a longer period while the latter two are intensive and short. Although the peak dates for both years are exactly the same, the median date of passage is 9 days later in 2002 than in 2003. The total phenology data of Willow Warbler passing through Cernek station in Kızılırmak Delta, Samsun (Northern Turkey) also reveals the same difference between median dates for the same years; 2002 median passage date being 9 days later than 2003 (OMU/OAM, unpubl.data).

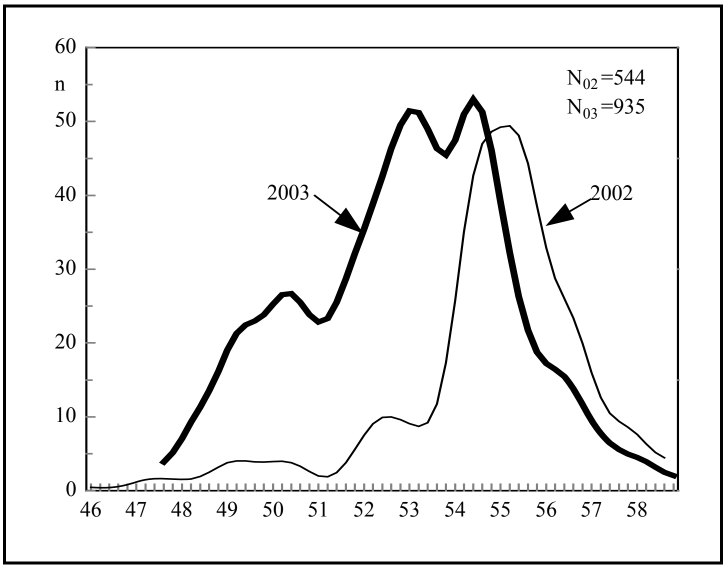

Figure 3.1 Comparison of total seasonal dynamics in autumn 2002 and 2003. The x axis represents time period as pentads which are 5 day periods numbered in order starting from 1st of January in a full year system (See Appendix C for pentad details). If not stated otherwise all migration dynamics (phenologies) are smoothed 4 times.

3.2.2 Migration of sexes

In order to check if there is any sexual differentiation in migration of Willow Warblers passing through the study area, the phenology data of male and female Willow Warblers (in regardless of age classes) were analyzed. This analysis was carried out only for 2003 since sample size was larger for that year. As is clear in Figure 3.2, there is no obvious differentiation in migration dynamics of sexes in 2003.

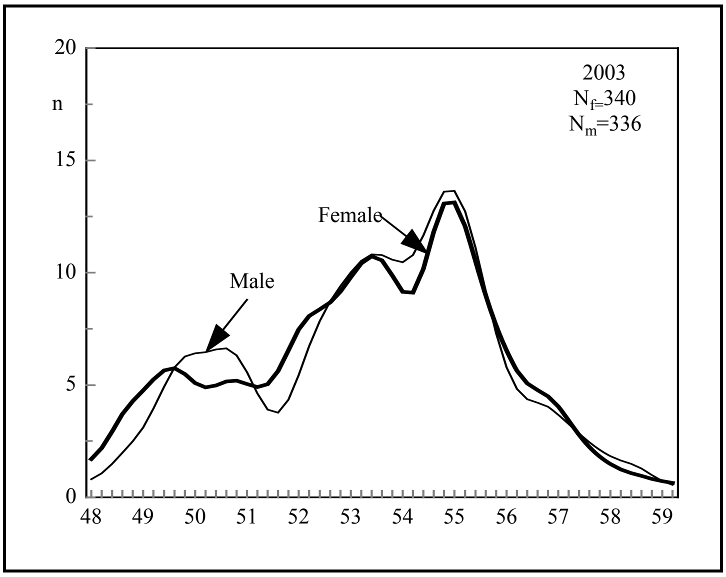

Figure 3.2 Autumn migration dynamics of males and females in 2003.

3.2.3 Migration of age groups

In 2002 the migration of immatures and adults peaked on 27th of September and 2nd of October respectively. Similarly there is a 5 day difference between the median dates of passage for age groups in 2002 with immatures earlier than adults. In 2003, the migration of adults and immatures peaked on 17th and 27th of September respectively whereas the median days of passage for age groups are the same (Table 3.2).

As for age specific differences throughout the study period cumulative passage data for each year and age groups were analysed (Figure 3.3). In 2002 until 52nd pentad, adult and immature passages are synchronised although afterwards there is a heavier passage of immatures. The passage of age groups become sychronised again towards the end of the study period. In 2003, however, the passage is unsychronized till about 53rd pentad with a heavier passage of immatures. The passage of age groups after this period is in synchrony till the end of the study period as also shown by dates for median passage.

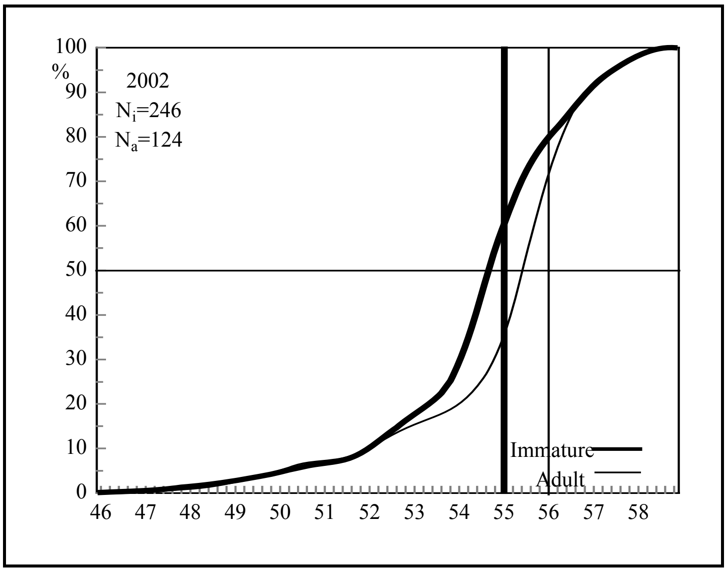

Figure 3.3 Total seasonal dynamics of adults and immatures in 2002 (shown as daily cumulative percentage). The vertical axis marks the median dates of passage, bold line is immature, thin line is adult.

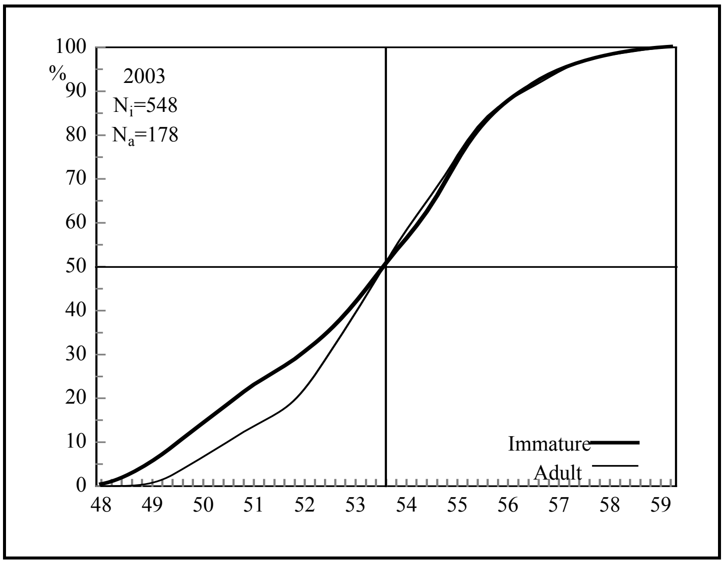

Figure 3.4 Total seasonal dynamics of adults and immatures in 2003 (shown as daily cumulative percentage). The vertical axis marks the median dates of passage, bold line is immature, thin line is adult.

3.3 Biometrical characteristics of migrants

3.3.1 Wing length

The wing length of all captured Willow Warblers range from 60 to 75 mm and 57 to 79 mm in 2002 and 2003 respectively. For 2003, two individuals with wing lengths of 57 mm and 79 mm were considered outliers and excluded from the analysis (Figure 2.7). Wing length differs from individual to individual based on age, sex and geographic origin. The descriptive statistics for wing length of distinct age and sex classes are provided in Table 3.3. The difference between wing length of sex groups are larger than the difference of wing length between age groups with adult and male wings being on average longer than immature and female wings respectively.

3.3.2 Tail length

The descriptive statistics for tail length of distinct age and sex classes are provided in Table 3.2. The tail length of all captured Willow Warblers range from 40 to 58 mm and 46 to 64 mm in 2002 and 2003 respectively. Similar to the wing length the difference between tail length of sex groups are larger than the difference of tail length between age groups with adult and male tails being on average longer than immature and female wings respectively.

Table 3.3 Wing length, tail length, body mass and fat score of birds caught in 2002 and 2003 according to age and sex groups.

	Mean ± SE (SD)				
	Sample size	Wing length (mm)	Tail length (mm)	Body mass on first capture(g)	Fat score on first capture (0-8)
2002 (all)	544	66.86 ± 0.13 (3.09) n=540	50.32 ± 0.13 (2.93) n=529	11.38 ± 0.07 (1.63) n=535	4.63 ± 0.06 (1.47) n=541
Adults	124	67.77 ± 0.29 (3.17) n=124	51.03 ± 0.27 (3.00) n=120	11.39 ± 0.14 (1.57) n=123	4.61 ± 0.14 (1.52) n=123
Immatures	246	66.27 ± 0.19 (2.99) n=244	49.79 ± 0.19 (2.93) n=242	11.45 ± 0.11 (1.70) n=240	4.67 ± 0.09 (1.43) n=244
Adult female	61	64.93 ± 0.17 (1.29) n=61	48.90 ± 0.25 (1.89) n=58	10.80 ± 0.18 (1.40) n=60	4.63 ± 0.21 (1.615) n = 60
Adult male	52	71.06 ± 0.18 (1.30) n=52	53.71 ± 0.26 (1.84) n=51	11.97 ± 0.20 (1.47) n=52	4.58 ± 0.18 (1.33) n = 52
Immature females	108	63.41 ± 0.12 (1.28) n=108	47.84 ± 0.21 (2.19) n=107	10.90 ± 0.16 (1.60) n=105	4.65 ± 0.15 (1.60) n = 107
Immature males	116	68.98 ± 0.14 (1.47) n=116	51.85 ± 0.19 (2.07) n=114	11.95 ± 0.16 (1.66) n=114	4.70 ± 0.12 (1.31) n = 116
2003 (all)	935	66.58 ± 0.10 (2.94) n=919	54.82 ± 0.11 (3.23) n=916	10.37 ± 0.05 (1.61) n=930	3.85 ± 0.05 (1.62) n=929
Adults	178	67.29 ± 0.25 (3.22) n=173	55.73 ± 0.26 (3.43) n=175	10.54 ± 0.12 (1.62) n=177	4.08 ± 0.12 (1.62) n = 177
Immatures	548	66.10 ± 0.12 (2.79) n=545	54.35 ± 0.13 (3.08) n=541	10.25 ± 0.07 (1.61) n=545	3.75 ± 0.07 (1.62) n =546
Adult female	91	64.55 ± 0.16 (1.50) n=91	53.57 ± 0.27 (2.57) n=90	10.14 ± 0.16 (1.50) n=90	4.34 ± 0.17 (1.62) n = 90
Adult male	77	70.49 ± 0.14 (1.20) n=77	58.27 ± 0.29 (2.58) n=77	11.01 ± 0.19 (1.64) n=78	3.81 ± 0.18 (1.56) n = 77
Immature females	249	63.45 ± 0.08 (1.19) n=249	52.14 ± 0.15 (2.33) n=245	9.84 ± 0.10 (1.52) n=247	3.96 ± 0.10 (1.60) n = 233
Immature males	257	68.69 ± 0.08 (1.24) n=257	56.40 ± 0.14 (2.29) n=253	10.60 ± 0.10 (1.54) n=255	3.53 ± 0.10 (1.60) n = 255

3.3.3 Body mass and fat load

In 2002 fat scores of birds captured show a unimodal distribution with a peak of T5 birds which is also the median fat class. In 2002 the majority of the birds on first capture have fat class 5 and above (67.65 %). Unless clearly stated otherwise, all values are of birds measured when they were first captured.

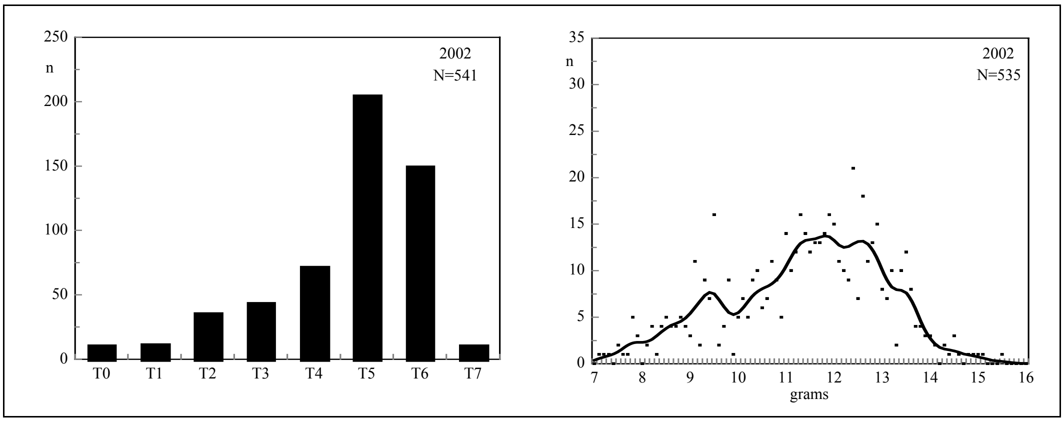

Figure 3.5 The distribution of fat classes and actual body mass in 2002. Abbreviation T is used for fat classes (i.e TX means birds with fat class X).

Fat scores of birds captured in 2003 however show a bimodal distribution with peaks of T5 and T2 birds, respectively, while the lowest and highest four fat classes are very infrequent. The median fat class is T4. In 2003 the percentage of birds on first capture with fat class 5 and above is 45.53 % .

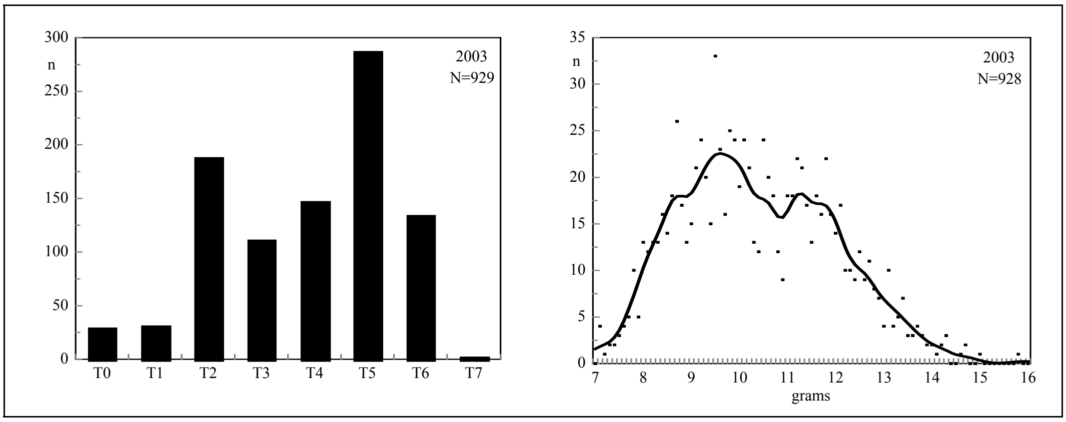

Figure 3.6 The distribution of fat classes and actual body mass in 2003.

The mean fat score for birds on arrival in 2002 and 2003 is 4.63±0.06 (1.47, n=541) and 3.85±0.05 (1.62, n=929) respectively. For 2002 and 2003, the mean body mass on arrival is 11.38 ± 0.07 (1.63, n=535) and 10.37±0.05 (1.61, n=930) respectively. The differences between years for fat scores and body mass are highly significant ($p<0.001$, unpaired t test). The difference in years is also reflected in Figures 3.5 and 3.7 where 2002 birds are heavier on average than those of 2003.

The relationship between age groups and between years was analysed (Figure 3.7). For both years and for both adults and immatures fat class T5 dominates but the proportions of all fat classes reveals a significant difference between years with higher proportions of T2 birds of both immature and adults in 2003. In 2003, the fat class distribution of immatures closely follows the overall frequency distribution with fat classes 5 and 2 being the top two classes in frequency. The adults with fat class 2 rank only 4th among all birds, so the fat class 2 wave in 2003 is clearly made up of immatures.

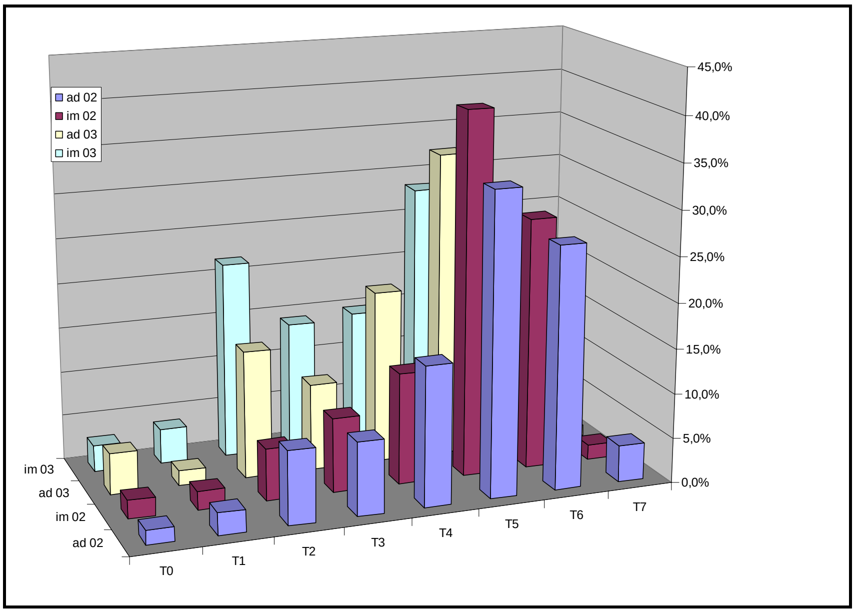

Figure 3.7 Comparison of fat score distribution between years and age groups (only arrival fat scores are included).

The change of fat class over time were also analysed for 2002 and 2003 (Figure 3.8). In 2002, birds with lower fat classes seem to dominate the first few weeks which corresponds to the time of ringing at Soltra substation where the ringing totals were low as is clear from large standard deviation. In both years, birds with highest fat classes were recorded in the second half of the migration period.

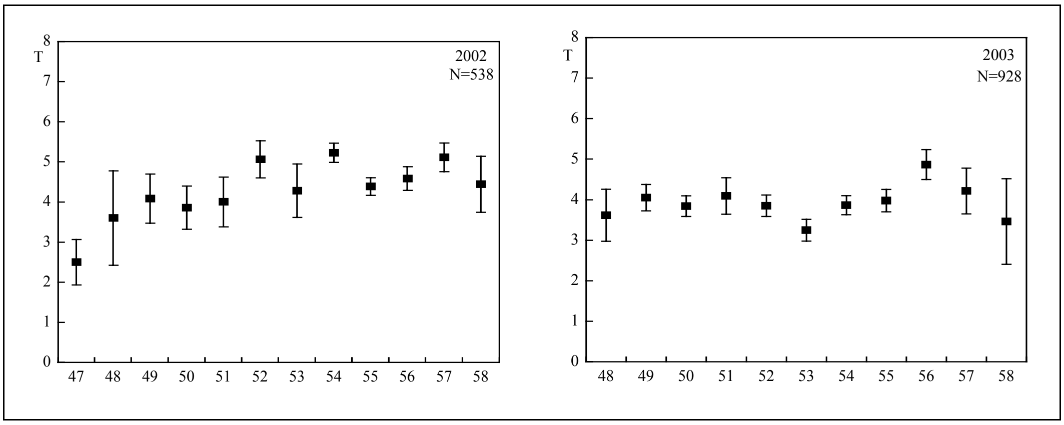

Figure 3.8 Fat class by pentads in 2002 (left) and 2003 (right) (mean value and SE*1.96 per pentad).

3.4 Age and sex differences of fat score

The change of fat class through the migration period was also checked for sex and age differentiation. Seperation of each sex into age groups yield too small a sample size for 2002 Therefore the analysis was done only for 2003.

For females the sample size for adults is much lower than the immatures as clear from large standart deviation especially in the first half of the migration period. That makes comparison difficult, however the trend for the latter half of the migration period between these age groups seem to differ (Figure 3.9).

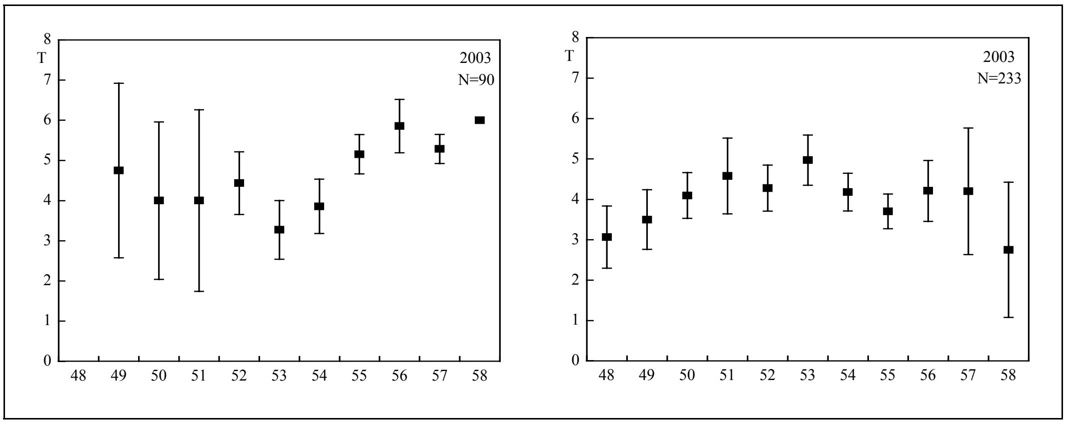

Figure 3.9 Fat class by pentades for adult (left) and immature (right) females in 2003.

Similarly the sample size for adult males is much lower than the immature males. Figure 3.10 does not show a clear trend between age groups of males in 2003 migration period.

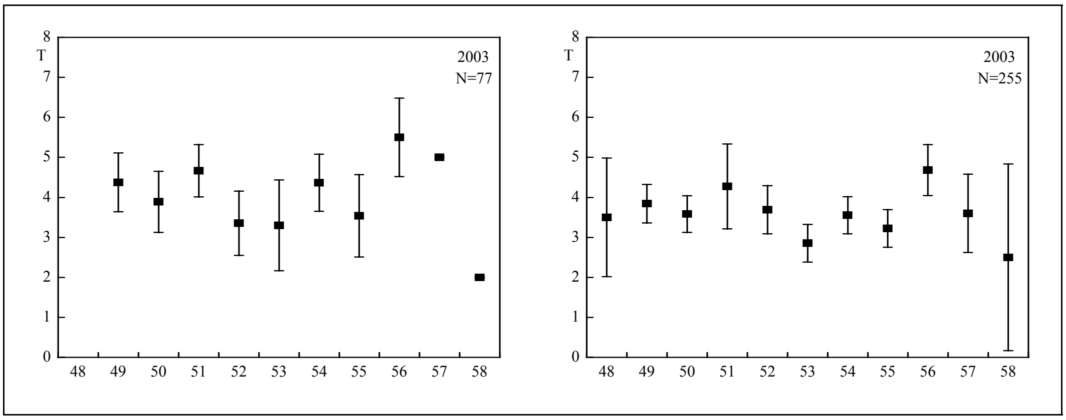

Figure 3.10 Fat class by pentades for adult (left) and immature (right) males in 2003.

The fat class change throughout the migration period was compared between sexes for each age class (Figure 3.11). Both adult and immature females are found to be slightly fatter than males during most of the migration period except for immature males being fatter than females in the first two pentads and adults being of nearly equal fatness in the first half of the season. Adult males are about 8.5% heavier (Table 3.3) but have an average fat score that is 87% of that of adult females. Similarly immature males are 7.5% heavier but carry 89% of the fat load of an average immature female. Therefore, although males of any age are heavier (i.e. larger) their fat loads are lower.

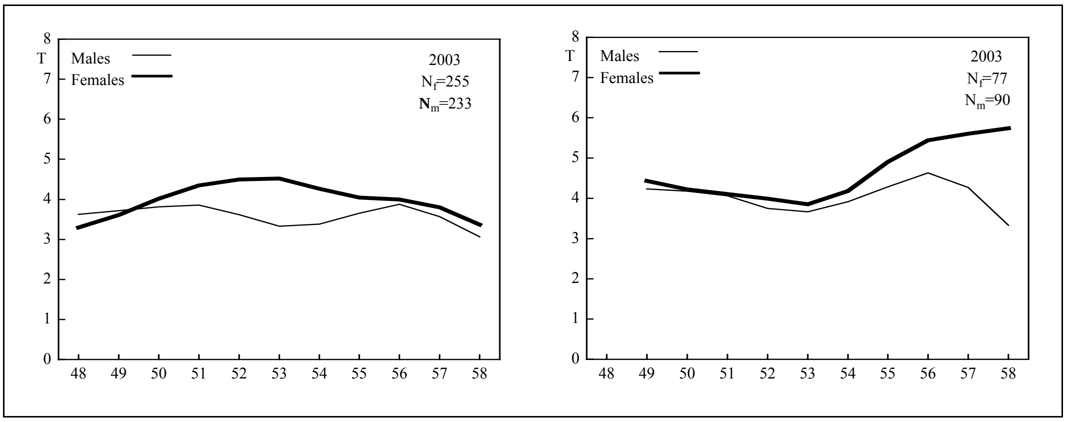

Figure 3.11 Comparison of fat class by pentades for immature males and females (left) and adult males and females (right) in 2003

3.5 Migration of fat-score groups

The frequency distribution graph of fat classes in 2003 was bimodal with peaks of fat class 5 (T5) and fat class 2 (T2) respectively. Further analysis of these fat classes were carried out looking at their phenologies.

Figure 3.12 shows a differentiation in phenologies of these two fat classes with a clearly heavier passage of T5 for most of the study period except for a period that corresponds to late September (between 15th and 25th which also corresponds to the second migration peak in total phenology).

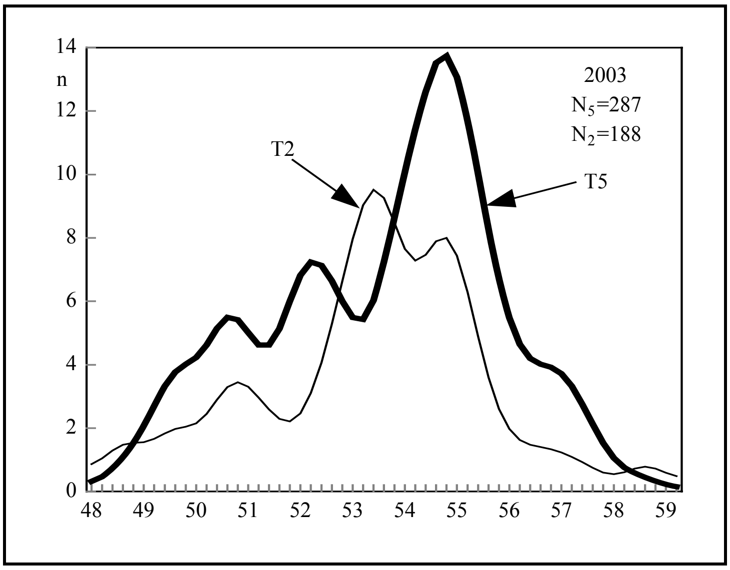

Figure 3.12 Total seasonal dynamics of fat classes 2 and 5 in 2003.

The ratio of T5 to T2 birds show significant changes over time, with an excess of T2 birds at the middle of the migration season around late September, and an excess of T5 birds before and after (Fig 3.13).

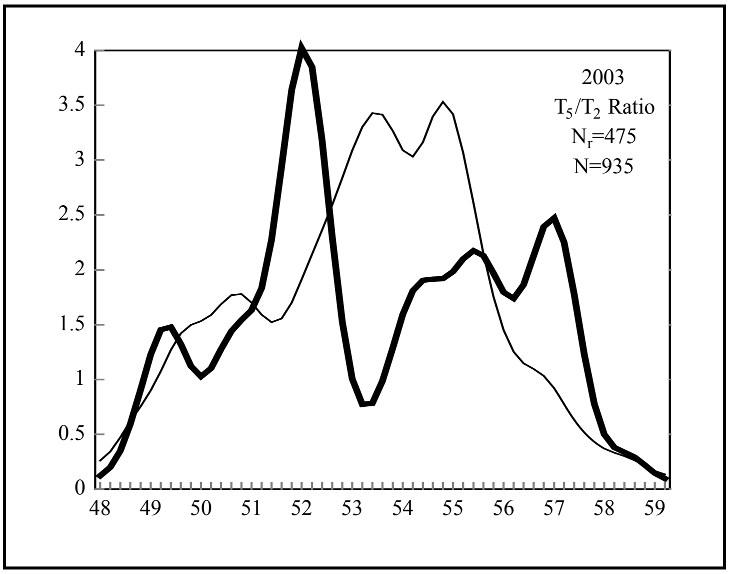

Figure 3.13 The ratio of T2 and T5 in 2003 against the total phenology.

3.6 Stopover Behaviour

3.6.1 Length of the stopover

The number of birds that were retrapped was 50 and 112 for the years 2002 and 2003 respectively. In 2002 the stopover range of retrapped Willow Warblers was 1-15 days and the median stopover length was 5 days. Similarly in 2003, the stopover range was 1-16 days and the median stopover length was 5 days (Table 3.4). It must be born in mind however that the time difference between the first and last captures of retrapped birds provides only a minimum estimate of stopover length since the individual might have arrived earlier and/or departed later.

Table 3.4 Stopover length details of retrapped birds in 2002 and 2003.

Year	Minimum stopover range	Median stopover length
2002 (n=50)	1-15 days	5 days
2003 (n =112)	1-16 days	5 days

For 2003, the distribution of stopover length of retrapped birds was also analysed. The majority of birds stay five days or less with maximum number of birds (n=20) staying for only 2 days. The maximum days of stay on the other hand is 16 days although only 6 birds stay more than 11 days (Figure 3.14).

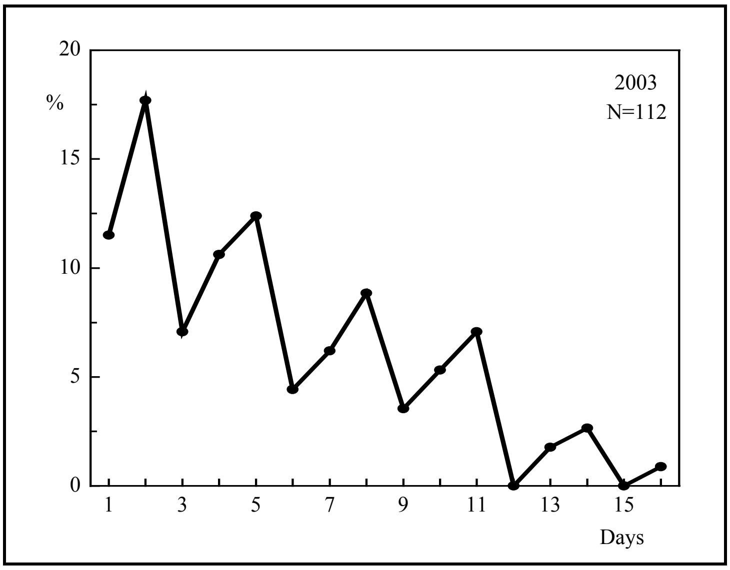

Figure 3.14 Distribution of stopover lengths in 2003 (raw data). The x axis shows the length of stay as number of days between first and last capture dates (minimum stopover range).

3.6.2 Migration of retrapped and never retrapped birds

For 2003 the relationship between migration dynamics of birds that were only captured once during the migration season (never retrapped) and birds that were retrapped was investigated.

The majority of the retrapped birds are captured in the middle of the migration season whereas never retrapped birds come in several waves starting from the beginning of the migration season (Figure 3.15). The ratio of the retrapped birds to the never retrapped birds was graphed against the total migration dynamics of Willow Warblers in 2003 (Figure 3.16). This figure shows that the first peak of the total migration dynamics is made up mostly of not retrapped birds while the first of the latter 2 more intensive peaks are made up mostly of retrapped birds. The last peak of the total seasonal dynamics seem to be made up of peaks of both bird groups.

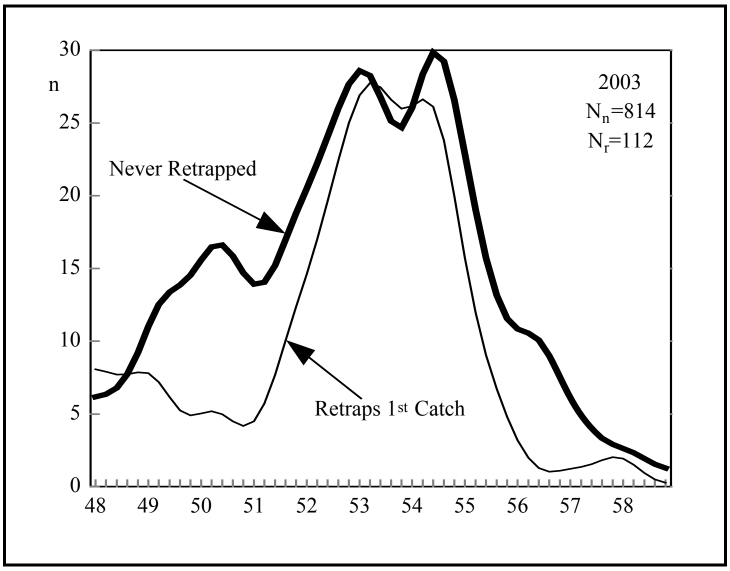

Figure 3.15 Total seasonal dynamics of never retrapped and retrapped birds in 2003.

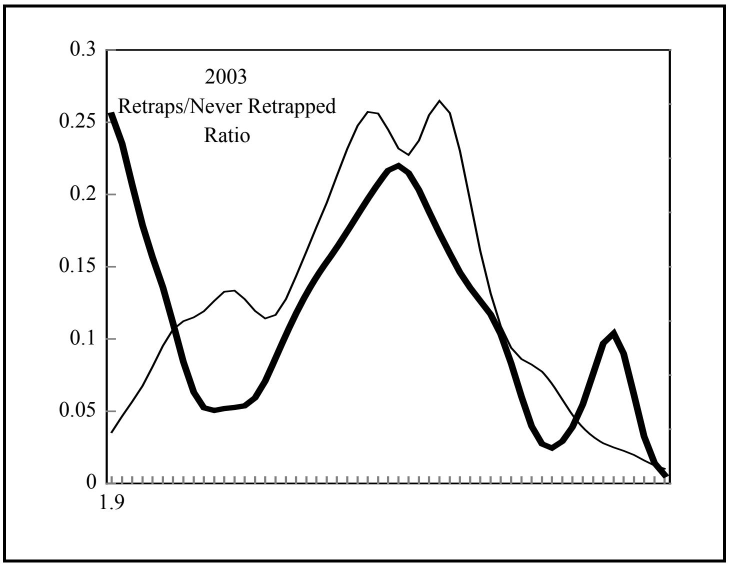

Figure 3.16 Total seasonal dynamics of the ratio between never retrapped and retrapped in 2003 with total migration phenology graph in the background.

3.6.3 Detailed pattern of stopover

In 2002, 50 birds were retrapped in 62 occasions. Figure 3.17 presents fat class changes of individuals which have been retrapped over time.

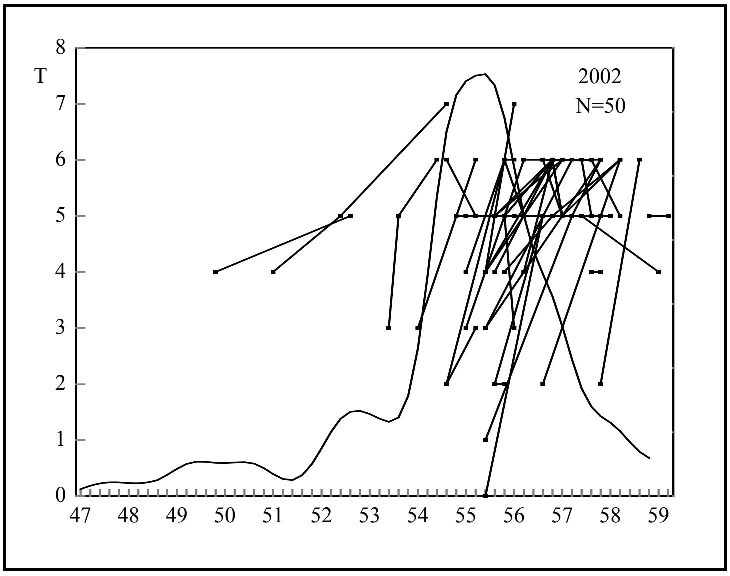

Figure 3.17 Fat class changes of retrapped individuals in 2002 against general phenology.

In 2002 there is only 1 retrap each belonging to T0 and T1 fat classes on first capture. As can be seen from Figure 3.17, both of these birds gained significant amounts of fat. The great majority of birds have increased their fat scores regardless of their initial fat load. Only a single bird got leaner as the season progressed.

In both 2002 and 2003, the mean body mass on first and last captures had significantly increased by 9.5% and 16.8% respectively. Similarly, average fat class values increased by 25.5% and 42.5% respectively. It is clear that the stopover habitat helped birds to put on significant fat and increase their body mass, especially in the 2003 migratory season.

Table 3.5 Body mass and fat class of retrapped birds (FC= first catch, LC= last catch)

Year	FC body mass Mean±SE (SD)	LC body mass Mean±SE (SD)	FC fat class Mean±SE (SD)	LC fat class Mean±SE (SD)
2002	10.81±0.20 (1.36) n=48	11.84±0.17 (1.22) n=50	4.24±0.21 (1.46) n=50	5.32±0.13 (0.94) n=50
2003	9.87±0.14 (1.49) n=112	11.53±0.15 (1.58) n=110	3.32±0.16 (1.72) n=111	4.73±0.14 (1.47) n=112

In both years, retrapped birds increased between their first and last captures both their body mass and fat scores but mean fattening rates did not differ between years (p=0.178, unpaired t test).

In 2003, 112 birds were retrapped on 133 occasions. Individual changes of fat scores and body mass are shown as separate fat classes (Figure 3.18 to 3.24).

In 2003 there were only 8 birds with fat class 0 that stopped over. All these lean individuals arrived during the middle of the migration passage, and gained significant amounts of fat. An exceptional individual gained more than twice its initial weight in a few days

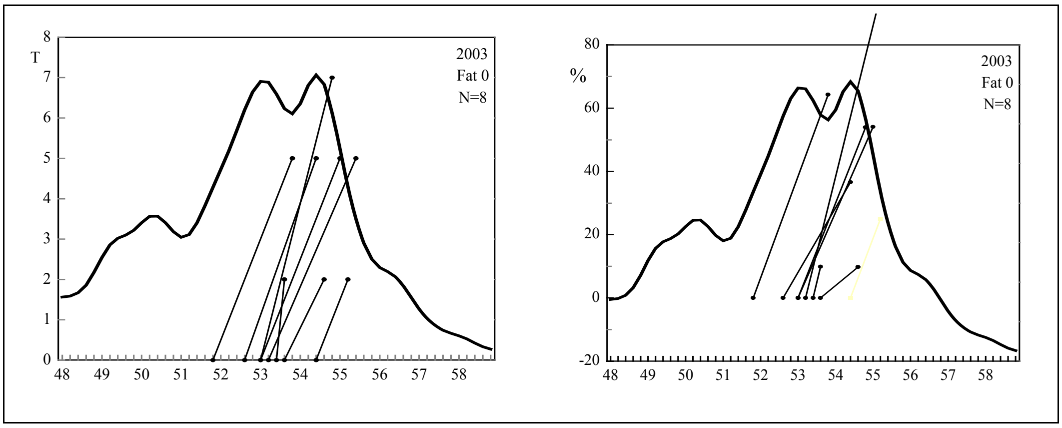

Figure 3.18 Fat score (left) and body mass (right) (%) change of T0 birds in 2003. Each line represents an individual Willow Warbler with start and end points of the line being first and last capture dates respectively while the angle of the line shows the degree of change. All graphs have total seasonal phenology for 2003.

In 2003 there were only 5 birds with fat class 1 that stopped over. These T1 birds that stopped over arrived during the middle of the migration passage. All except for one put on weight during their stay.

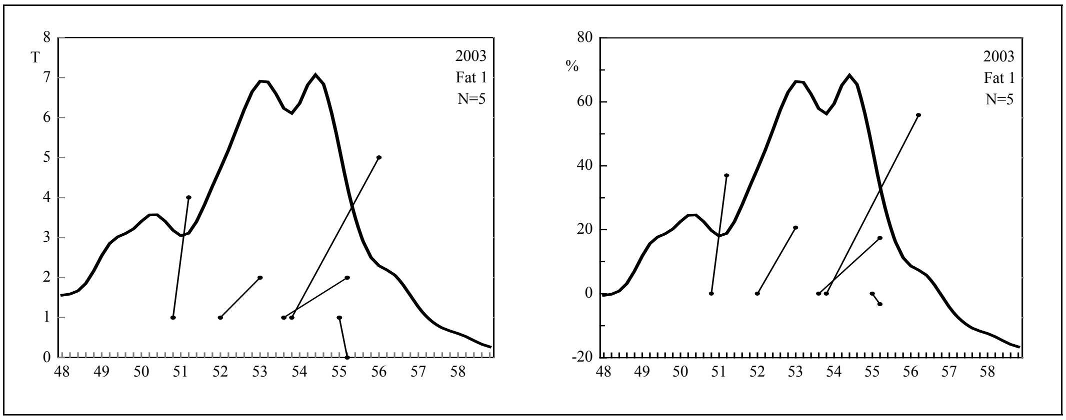

Figure 3.19 Fat score (left) and body mass (right) (%) change of T1 birds in 2003.

In 2003 there were 30 birds with fat class 2 that stopped over. These stopping over T2 birds show a distinct spacing of time of capture. Majority of these birds increase their fat classes to T5 –T6 and put on weight before departure.

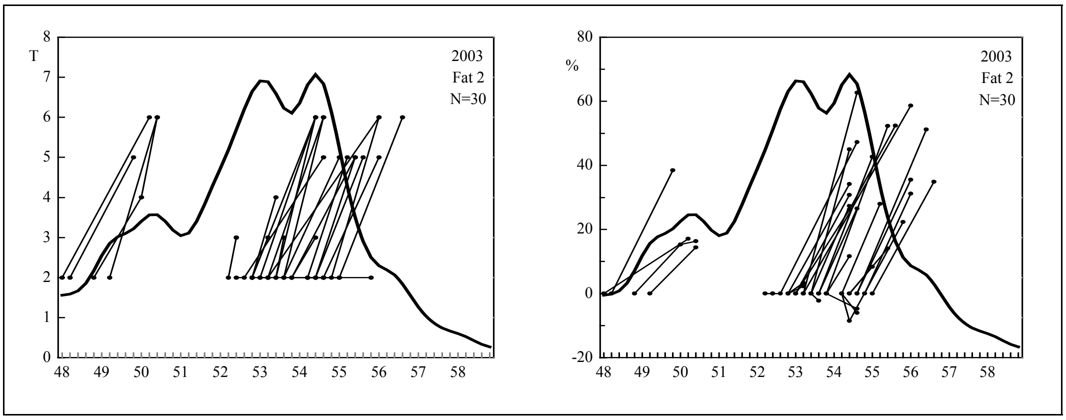

Figure 3.20 Fat score (left) and body mass (right) (%) change of T2 birds in 2003.

In 2003 there were only 11 birds with fat class 3 that stopped over. These T3 birds arrived in the beginning and middle of the migration passage. Six out of 11 birds increase their fat class to T6. One bird which could be unhealthy experienced a decrease both in fat class and % change of body mass. There is one other individual which experienced a 40% increase in body mass while the fat class dropped to T2. It is likely that fat class data was recorded wrongly either by the ringer or by the person who writes the data.

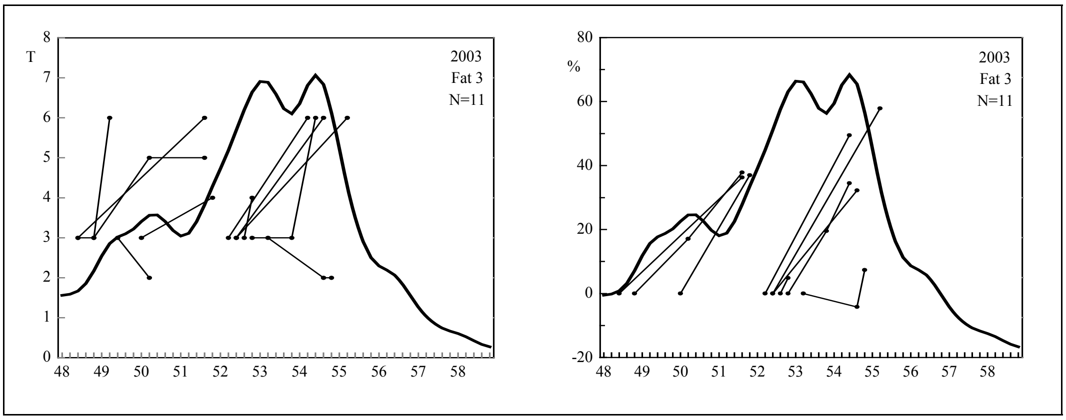

Figure 3.21 Fat score (left) and body mass (right) (%) change of T3 birds in 2003.

In 2003 there were 16 birds with fat class 4 that stopped over. These T4 birds seem to have arrived all throughout the migration passage except for the very end. Only 4 of these birds increase their body mass more than 25 %.

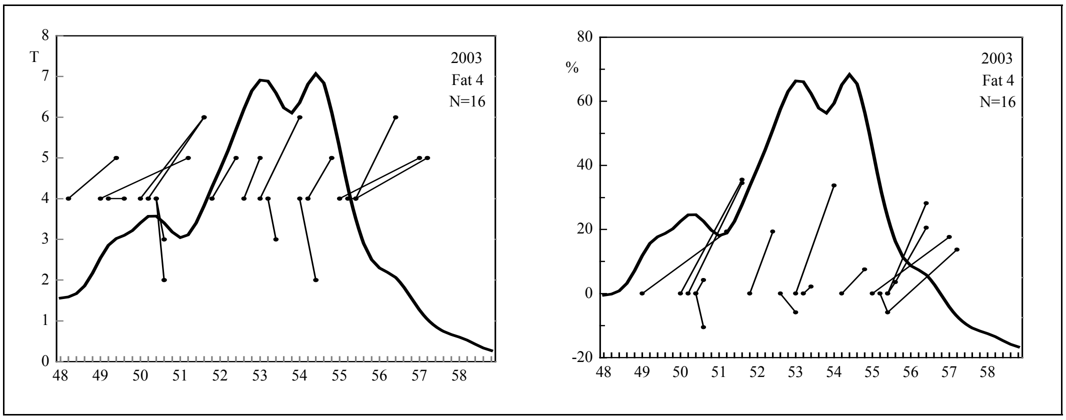

Figure 3.22 Fat score (left) and body mass (right) (%) change of T4 birds in 2003.

The second frequent fat class of retrapped birds in 2003 is T5. There are a total of 28 birds that arrived all throughout the season except for the beginning. Majority of the birds increased their fat class to T6 but only 4 of them experienced a body mass change of around 20 %. One other bird however increased its body mass almost by 40 %. There are a couple birds that significantly lost weight and fat class during stay. These birds are most likely the ones that will not be able to complete their migratory journey or they might be due to human errors in recording measurements.

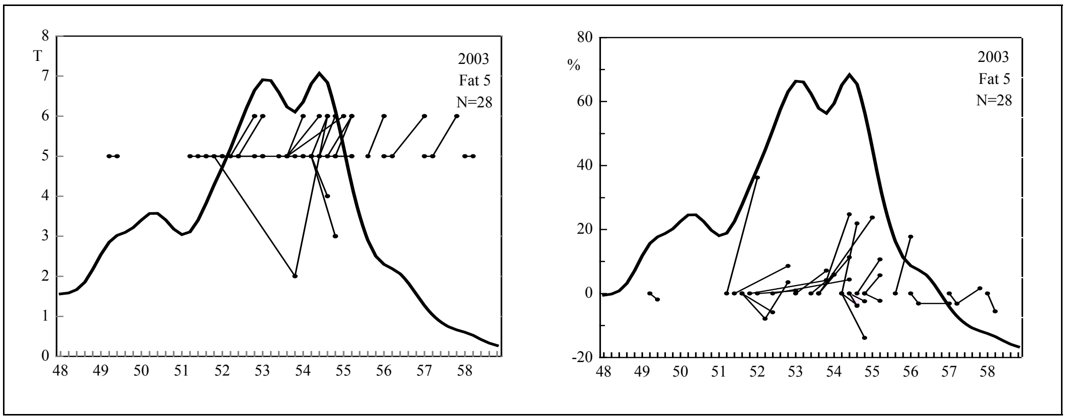

Figure 3.23 Fat score (left) and body mass (right) (%) change of T5 birds in 2003.

The number of retrapped individuals with fat class 6 in 2003 is 8. All arrived relatively later compared to other fat classes. Although 4 of them increased their body mass by around 10 %, the fat class did not change for these birds.

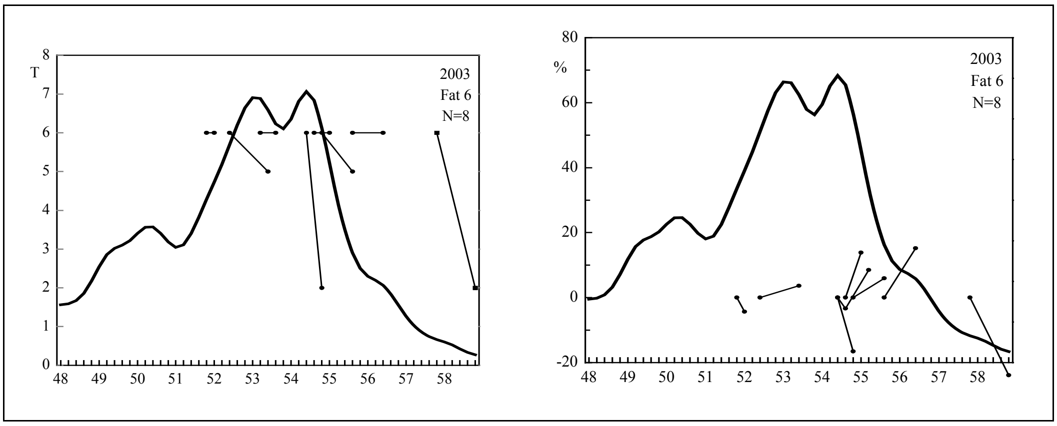

Figure 3.24 Fat score (left) and body mass (right) (%) change of T6 birds in 2003.

3.6.4 Average changes of fat load and body mass

Changes in body fat have been compared through calculating standardized weights (See 2.4 for details). Figure 3.25 shows the pattern of fat load change (in grams) following initial capture of retrapped individuals. The birds slightly lose weight (fat) for up to 2 days after first capture but then put on weight in an increasing rate until the ninth or tenth day after first capture. Fat load change in grams was highest when the stopover length was 10 days. There were very few birds that stayed more than 12 days therefore in the graph stopover length equal or more than 12 days were combined.

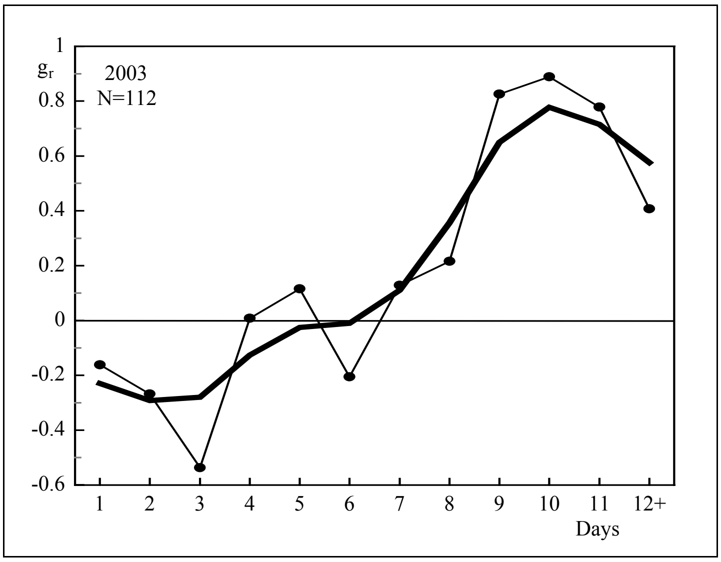

Figure 3.25 Fat load change in grams of retrapped birds in 2003 (Raw vs smoothed).

Figure 3.26 shows the actual body mass change of the birds that were retrapped in 2003. The stopping over birds increase their body mass during their stay. Maximum change is experienced by the birds that stopover for 14 days.

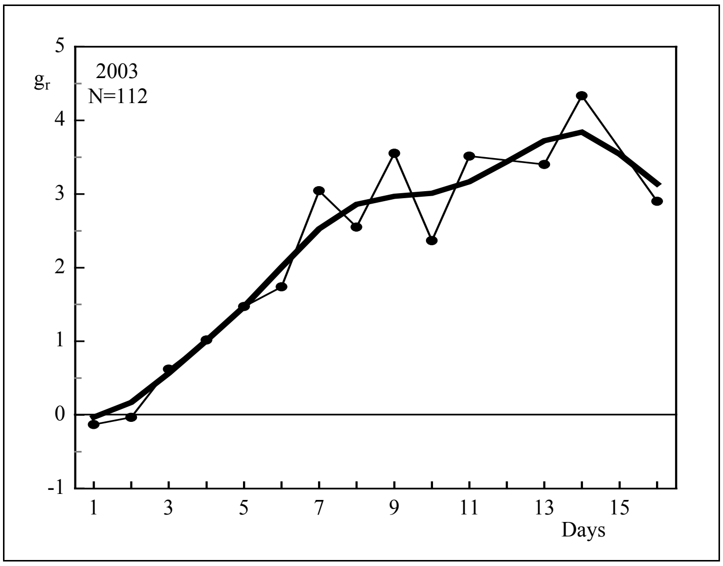

Figure 3.26 Actual body mass change in birds stopping over in 2003.

3.6.5 Age specific differences in stopover behaviour

The age specific differences in stopover behaviour of retrapped Willow Warblers in 2003 was analysed. The stopover range is found to be similar for both age groups. Although the median stopover length for age groups are the same, the adults on the average stay longer than the immatures (Table 3.6).

Table 3.6 Stopover details of retrapped birds in 2003 according to age groups.

	Minimum stopover range	Median stopover length	Mean stopover length
Adult (n=16)	1-14 days	5 days	6.25 days
Immature (n =77)	1-16 days	5 days	5.53 days

The mean change in actual body mass of adults and immatures is 17.93 gr and 12.85 gr respectively (Table 3.7). The mean stopover length for adults and immatures are 6.25 and 5.53 days respectively. Thus mean body weight increase (in grams) per stopover day is 0.30 for adults and 0.23 for immatures. This means that the adults put on fat (and weight) during stopover at a faster rate than do the immatures.

Table 3.7 Body mass and fat class of retrapped birds in 2003 according to age groups

	Mean fat score change	Mean body mass change (gr)	Mean stopover length (days)	Average gain/day (gr)
Adult (n=16)	1.88	17.93	6.25	2.87
Immature (n=77)	1.28	12.85	5.53	2.32

CHAPTER 4

DISCUSSION

4.1 Critique of the methodology

During ringing studies the birds that actively migrate at night are caught and ringed during the day when they have landed after migrating at night. While providing the researcher with information on species composition and the degree of nocturnal passage, this method could lead to complications during interpretation of the results (Alerstam 1990). Despite the fact that sample of caught birds represents resting or foraging ones rather then active migrants, it is considered that catching dynamics of small passerines reflects their migration dynamics relatively well (Nowakowski 1999).

According to Busse (2000) there are several essential methodological requirements in order to stabilize catching effort in ringing studies both within a season and on a long-term scale: 1) Time and period of work should be standardized. 2) The quality and number of nets should be stable within the study season and between the years. 3) The daily catching routine should be stable; preferably continous throughout the day without closing the nets for the night since daily phenologies could change according to locality. 4) The changes to the catching habitat should be minimised.

4.1.1 Effort and continuity

In 2002 the study initially started at Soltra substation but had to be moved to Kuşcenneti National Park due to a very low daily catch. This inevitably affected the continuity of the study at one location and made it impossible to get a precise picture of migration dynamics of Willow Warbler for that autumn. In 2003 due to logistical problems the ringing study could only start on 26th of August, leading to missing of the beginning of the passage. Apart from the change of locality in 2002 and a late start in 2003, the passage of Willow Warbler through the study area was fully documented. In both years the study was carried out continuously throughout the day and the study period, except for days when weather did not permit any catching to take place.

The total net length was comparable between the years after at least the middle of September. The placement of nets between the years however was not exactly the same since especially in 2002 the team had less experience with the habitat and eventually some of the nets with low capacity later had to be moved elsewhere. In 2002 the team had already lost some part of the study period in Soltra and therefore had no extra time to make an ideal pathway for nets control in the dense vegetation of the national park, whereas in the beginning of 2003 extra effort was spent for this task leading to different placement of several nets between years. However, overall the differences are limited to a small part of the period or are not expected to cause any significant variation.

4.1.2 Ringer differences

Although measurements are taken in a standard manner by all ringers at the study station, it may sometimes be possible that a consistent bias may exist in some cases. In 2002, up to ten different ringers have measured birds but in general personal differences are considered to be negligible. In 2003 the majority of the measurements (98.4 %) were carried out by two ringers (the M.Sc. candidate & J. Didrickson). To test whether there is any difference between the ringers, the values for wings and tails of the same birds measured by these two ringers were compared. Although there were statistically significant differences ($n=46$, $p<0.001$, two-tailed t-test) absolute differences were only 0.39 and 1.40 mm for wing length and tail length, respectively. These differences are clearly biologically not important, therefore no corrections were carried out. Moreover the measurement bias is smaller than half the minimum unit (i.e. 1 mm) used for wing length measurements so it does not effect the outcome.

4.1.3 Sex determination

Wing length of Willow Warblers is known to differ from individual to individual based on age, sex and geographical origin (Cramp 1992). With the knowledge of adult birds being longer winged than the immature birds and that males Willow Warblers are larger than females, the birds captured were sexed according to a wing length based criteria developed seperately for each age group. For both adults and immatures, two peaks in wing-length distribution graphs were discernible, presumably representing different sex classes. Following this assumption, the range of values representing peaks for each age group was taken as a criteria to allocate each bird to a sex class.

According to this method some birds could have been placed in wrong sex classes, therefore leading to misinpretation of the data. However, the difference used in this study (between two peaks presumably representing males and females in the wing length graph) is the same as given in Cramp (1992). Nevertheless, some individuals will inevitably allocated to the wrong sex class because of the simplicity of the method used and the variability of wing length for populations. The exclusion of birds with an intermediate wing length, and therefore of ambigous membership to either sex, reduces the probability of such mistakes.

Measurement mistakes or ringer bias could also contribute to allocation of birds to wrong sex classes. However large sample sizes and exclusion of outliers from wing length measurements reduce the likeliness of these factors causing a significant bias.

4.2 Capture statistics

The total numbers of ringed Willow Warblers were 543 and 929 for years 2002 and 2003, respectively Although the study was carried out for a longer period in 2002, the total number of birds ringed this year is much lower than in 2003. In 2002, between 16th of August and 12th of September ringing was carried out in Soltra substation and on 14th of September the study was moved to Manyas Kuşcenneti National Park substation due to low autumn migration activity of passerines in Soltra in general (only 26 Willow Warblers were captured at Soltra substation). Therefore, the difference in the total number of the study species ringed in 2002 despite a longer period of study could be due to the unsuitable habitat of Soltra substation for migrating Willow Warblers in autumn.

The percentage of retrapped birds for these two years should be compared with caution since the study in 2002 starts at Manyas Kuşcenneti National Park substation only in mid-September; 18 days later than in 2003. Therefore, the shorter period of ringing activity at the start of ringing at the park in 2002 meant lower retrapping possibilities, although two birds that have been ringed in Soltra in 2002 have been retrapped at the National Park 7 and 14 days later. The Soltra substation is only 3 km away from the National Park substation. Probably the birds that land in Soltra quickly disperse to the more suitable stopover habitats in the vicinity.

4.3 Seasonal dynamics of migration

4.3.1 Overall pattern of migration

The results of this study show that Willow Warblers migrate through Manyas Kuşcenneti National Park from mid-August to end of October. Passage seems to be most intense from early September to early October. However since this study period does not cover the whole autumn migration period of the species and since it is only a data set of two years, it might be premature to try to characterise the passage migration dynamics. Larger data sets covering several additional years is necessary to fully understand the migratory pattern. At the Bosphorus (Istanbul), Porter (1983) reported Willow Warbler as the commonest migrant on many days between 6 August and early September with the latest individual observed as late as 29th of October. This further emphasizes that in future studies, fieldwork should ideally start at the beginning of August in order to have a full picture of Willow Warblers utilising Manyas Kuşcenneti National Park. The high numbers of birds captured is in accordance with literature which states that the species is abundant in east Mediterrenean in autumn (Cramp 1992).

The general phenology graphs for 2002 and 2003 reveal peaks which may possibly correspond to separate migration waves that represent different populations or age or sex groups with separate migration strategies, especially observed as a difference in timing of migration. The difference in autumn migration timing of Willow Warblers has been reported with longer-winged northern populations (subspecies *acredula*) migrating later than shorter-winged southern (nominate subspecies) populations (Hedenström and Pettersson 1984). As for age related differentiation of autumn migration of the species, immatures are initially ahead of adults due to earlier departure from the natal area although by the of end of August adults catch up with or get ahead (more southerly) of immatures (Hedenström and Pettersson 1987). Additionally, juveniles of subspecies *acredula* is reported to start the autumn migration earlier than juveniles of subspecies *throchilus* (Lindström *et. al* 1996). No sexual differentiation was observed in migration timing of adults (Niemeyer 1969, Lindström *et. al* 1996)

An exact comparison of Willow Warbler migration dynamics at Manyas Kuşcenneti National Park between years 2002 and 2003 is not possible before mid-September due to a time gap of nearly 20 days between start dates of ringing at this substation in consecutive years. The disparity in the number of birds captured between years could partly be due to this difference in the study duration between years in the more suitable habitat of Manyas Kuşcenneti National Park substation. Net placement was also slightly different in 2003 probably resulting in marginally higher capture per effort than 2002. Nevertheless, the almost two-fold observed difference in capture totals of 2002 and 2003 seems too large to be only caused by these factors. One reason could be local changes in migratory behaviour due to weather conditions. Certain local weather conditions may lead a large landfall that may cause differences between consecutive years (Alerstam 2006).

Another (non-competing) explanation is caused by a difference in the timing of passage of Willow Warblers through the area between years. The difference in median dates of passage between years with 2002 passage being 9 days later also supports this. The median dates of Willow Warbler through Kızılırmak Delta in Samsun in 2002 and 2003 are also different by 9 days, with the 2002 passage being later (OMU/OAM, unpubl.data). This general pattern between stations for the same two years also supports the suggestion that the difference in passage timing between years is unlikely to be caused only by differential sampling effort at the stations in those years.

4.3.2 Migration of sexes

In this study the data for 2003 was analysed for sex groups and no obvious differentiation in migration dynamics was found.

Similarly, in one autumn study in Sweden, no significant differences were found between average trapping dates of male and female adults (Lindström *et al.* 1996). Similar pattern for autumn was found by Niemeyer (1969) for passage through Helgoland in northern Germany.

The analysis was done with all age groups combined, so any possible differentiation of migration patterns of sex classes might have been masked by age groups differentiation. For Willow Warblers, sexual segregation of migration has been shown for spring with females arriving at breeding grounds later than males (Norman and Norman 1986, Tynjälä *et al.* 1993) which is assumed to be a migration strategy related to breeding, with males arriving early to occupy the best territories and females arriving late trying to be in good condition for breeding (Tynjälä *et al.* 1993). Probably no such pressures exist during the autumn migration and Willow Warblers are known to be highly adaptable in winter grounds (Cramp 1992).

4.3.3 Migration of age-groups

The cumulative passage graphs for different age groups reveal a difference in intensity of passage at the beginning of the study period in 2003 and towards the end of the study period in 2002. The synychronised passage of age groups until pentad 52 is difficult to interpret due to low sample size (n=41) during that period. In 2003 passage of immature birds is heavier until around pentad 53 when adults catch up with immatures.

These results are in agreement with the available data documenting later average passage for adults than immatures (Norman and Norman 1985, Lindström *et al.* 1996) in autumn. There are also studies which document that as season progress the adults catch up with or pass immatures through continental Europe (Hedenström and Pettersson 1987). However, several waves of populations may confound the observed patterns for particular age groups.

4.4 Biometrical characteristics of migrants

4.4.1 Wing length

In the light of our biometrical results of wing length and the available literature, it seems likely that more than one subspecies of Willow Warbler pass through Manyas Kuşcenneti in autumn but subspecies *acredula* dominates the catch. There is an average of 1.5 mm difference in the wing lengths of *trochilus* and *acredula* individuals (Bensch *et al.* 1999, Cramp 1992) which is much less than that observed between sexes.

Ringing studies in Europe has demonstrated a migratory divide latitudinally across central Scandinavia between northern and southern populations of Willow Warblers (Bensch *et.al* 1999). Accordingly, in the autumn, birds from southern Scandinavia (nominate subspecies) migrate southwest whereas northern birds (subspecies *acredula*) migrate southeast. Some eastern populations of the nominate subspecies are also assumed to have a south-southeasterly migratory direction (Chamberlain *et al.* 2000). Turkey lies in a southeastern direction from Scandinavia and from findings of these studies subspecies *acredula* and eastern populations of *trochilus* are expected to pass through Turkey.

4.4.2 Tail length

Tail length on the other hand is not used as a base for sexing but it is a supportive character for size. The variability of tail measurements (in terms of coefficient of variance) were higher than for wing measurements (5.89% vs 4.42%). This may be due to differences in tail measurement methods among ringers, regrown tails after loss, or the less adaptive value of the tail (hence higher inherent variation).

4.4.3 Body mass and fat load

In 2002, the ringing study starts at Manyas Kuşcenneti National Park on 14th of September. The results from 2003 suggest that the birds captured during the first one or two weeks in 2002 could be individuals that have already stopped over for a period and gained fat. Therefore, more departure body mass values could have been included in 2002 estimates, leading to an increase in the mean values of body mass and fat class for that year. When the fat score distribution is analysed according to age groups (Figure 3.7), it is seen that T2 is the second most frequent fat class in 2003 whereas it is 4th most frequent in 2002. This finding supports the hypothesis that in 2002 most birds that were captured had arrived at Manyas Kuşcenneti National Park some time ago and gained fat since immatures significantly dominate the overall fat class distribution for both years.

The differences in mean body mass and fat values for the years 2002 and 2003 could be either due to different composition of individuals from different populations with separate migration strategies passing through Kuşcenneti in 2002 and 2003, or different physiological states of the same populations that were passing through. In one study which looked at the migratory state of several long-distance migrants during autumn migration in northeastern Bulgaria, the mean values of body mass and fat class for Willow Warbler in 2002 was similarly larger than those for 2003 (Ilieva and Zehtindjiev 2005).

In 2002, birds with lower fat classes seem to dominate the first few weeks, but sample sizes are too small to make a meaningful comparison with 2003 observations. In both years, birds with highest fat classes were recorded in the second half of the migration period.

4.5.3 Migration of fat-score groups

The frequency distribution graph of fat classes in 2003 was bimodal with peaks of fat class 5 (T5) and fat class 2 (T2) respectively. A further analysis of these fat classes was therefore crucial in understanding the body condition and stopover relationship of Willow Warblers passing through the study site.

The ratio of T5 to T2 birds show significant changes over time, with an excess of T2 birds at the middle of the migration season around late September, and an excess of T5 birds before and after (Fig 3.13). These changes may be representing particular waves of migratory populations that have different mean fat loads because they have separate migration strategies.

4.5 Stopover behaviour

4.5.1 Length of the stopover

The stopover habitats for migratory birds are of utmost importance since without refuelling they cannot continue their migratory journey (Alerstam 1990). The research on stopover ecology of migrants is therefore crucial for understanding migration dynamics of each species. Much research on stopover ecology were carried out for several species (e.g Reed Warbler *Acrocephalus scirpaceus*) but research on stopover behaviour immediately before and after crossing barriers is very rare (Yosef and Chernetsov 2005).

The minimum stopover duration range and median stopover length between years are almost the same. This might suggest that the Kuşcenneti National Park habitat has been similar between these years for exploitation of Willow Warblers that stop over. It could also mean that the stopover behaviour of Willow Warblers passing through Kuşcenneti National Park in these years are similar, which in turn implies that the composition of birds as far as age /sex groups and populations are concerned are fairly stable.

The distribution of stopover length of birds that were retrapped in 2003 shows a peculiar pattern (Figure 3.14) The pattern suggests an influx of birds roughly every 3 days which cannot be explained by any periodicity. A similar pattern was observed in several other species including Redstart (*Phoenicurus phoenicurus*) (P. Busse, pers.comm).

4.5.2 Migration of retrapped and never retrapped birds

Figure 3.26 suggests that birds that were not retrapped dominate the earlier captures whereas birds that arrive later stop over (become retrapped). The first migration wave in 2003 is probably made up of birds which might have interrupted their migratory journey briefly due to weather conditions. This can be the reason why these birds were not retrapped. This finding also supports the passage of two different populations with different migration strategies as had also been suggested by biometrics data on captured birds. As suggested by biometrical data, birds caught ranged from nominate *trochilus* to *yakutensis* breeding in northeast Siberia. These two subspecies and the intermediate *acredula* (which made up the majority of individuals caught) have very different migratory ranges and timing, hence dissimilar migratory strategies. Even within the subspecies *acredula*, distinct populations may have separate routes and timing of migration.

4.5.3 Detailed pattern of stopover

For both 2002 and 2003 the detailed pattern of stopover clearly shows that the birds that stopover at Manyas Kuşcenneti National Park successfully replenish their reserves for the rest of the autumn migration. It is obvious in the graphs that show changes in fat class and weight for each bird of each fat class in 2003 that birds which arrive in lower fat classes experience a significant change in especially fat class although the birds that arrive with already high fat scores (i.e T5, T6) do not experience as pronounced a change. However if the peaks of low and high fat classes (T2 and T5) indeed show group of birds with different migration strategies, then the final fattening of higher fat class birds could still be crucially important since these birds could be the ones that have intemittent flight strategy over the coming barriers. Furthermore even though landing in Sahara is possible and even at times necessary, birds will need good amount of fat reserves to survive the resource limited conditions at a desert (Berthold 1993, Biebach 1990). Additionally, the difference between classes are not equal in fat class categories, so the real fattening of higher fat classes should be compared with the observed obvious change of lower fat classes.

4.5.4 Average changes of fat load and body mass

The findings of this study suggest that most Willow Warblers that stopped over at Manyas Kuşcenneti National Park reached sufficient levels of fat stores and continued their migration within ten days or so. Any stay beyond this time seems to have caused a reversal (i.e weight loss) possibly because such individuals may be of suboptimal health.

It is known that lean body mass (including flight muscles) of especially long-distant migrants is quite dynamic over a short span of time (hours or days), and birds can store and use both lean mass and body mass during migration (e.g. Piersma 1990). No special storage tissue exists in migratory birds for protein, therefore protein metabolism during flight results in changes for organ and muscle masses. This condition is termed as "phenotypic flexibility". Generally such flexible organ size changes are experienced as organ size increases during fattening phases of premigration and stopover periods and decreases during active migration (Bauchinger *et al.* 2005). Although there is an increase in actual body mass within the first week of stopover (Figure 3.26), it is not reflected in fat load change in grams (Figure 3.25) since the gain may be converted into organ size enlargement.

Willow Warbler is known to have a fast refuelling capacity (Cramp 1992). In a study of autumn migration in west coast of Portugal, Willow Warbler was found to have a fattening rate significantly greater than zero when the median stopover length is only 3 days (Catry *et al.* 2004). Similarly, for 2003, the results yield a significantly positive (average 1.515 g; $p<0.001$) rate of fattening for birds with a median stopover length of 5 days. Furthermore retrapped birds continued to put on weight for the first two weeks of their stay. Body mass change was highest when the birds stopped for 14 days. Overall, the majority of the birds that stopped over both in 2002 and 2003 put on a significant ampunt of fat. These findings strongly suggests that the quality of Kuşcenneti National Park was high for Willow Warblers in autumn migration.

There is evidence that migrating Willow Warblers put on little weight and/or fat in the early stages of their migration at the northern latitudes. Average fat scores for migrating populations are found to vary between 8.2 and 8.8 grams in Ottenby (Sweden) (Akesson *et al.* 1995), in Bukowo (Poland) (P. Busse, pers.comm), and Helgoland (Germany) (Dierschke and Bindrich 2001). On the other hand birds captured in locations that are just before an ecological barrier are heavier and fatter (e.g. 10.9 g. at Karpathos island, Greece (Biebach 1990). The departure body mass of birds retrapped in Malta is also high in autumn (Sultana and Gauci 1986). Similarly, individuals captured at Manyas Kuşcenneti National Park – when compared to birds captured further north – are heavier and fatter, arrival body mass values being 11.38 g and 10.37 g in 2002 and 2003, respectively. The departure weights of the retraps further reveals the level of preparation of birds for barrier crossing (11.84 g and 11.53 g in 2002 and 2003). In a study of passerine migration at METU (Ankara, Central Turkey) which covered a similar period of study and followed the same methodology for fat scoring, 46 % of the captured Willow Warblers (n=170) had a fat score 6 and above in autumn 2002 (Keşaplı Can 2004). Willow Warblers that stopped at METU is significantly fatter than Willow Warblers that stopped at Manyas Kuşcenneti National Park as reflected by much lower percentage of birds with fat score 6 and above (29.6 % in 2002 and 14.5 % in 2003).

4.5.5 Age specific differences in stopover behaviour

There are several studies investigating age specific differences in stopover behaviour experienced such as differences in rate of attaining fat, weight and the length of stopover (Woodrey and Moore 1997, Yong *et.al* 1998, Rguibi- Idrissi *et.al* 2003)

The results show that at least in 2003 adults put on fat load and weight at a faster rate than immatures. The mean stopover length of adults is found to be higher than immatures in 2003. In one study which took place in Morocco, stopover length of immature Reed warblers (*Acrocephalus scirpaceus*) was found to be larger than that of adults(Rguibi- Idrissi *et.al* 2003). Similary in a study in New Mexico, USA, immature Wilson's Warbler (*Wilsonia pusilla*) stopped over longer than adults in autumn (Yong *et.al* 1998). Stopover behaviour of birds at a particular site is expected to reflect the migratory strategy of birds which is strongly affected by geography, particulary the distance from ecological barriers. Therefore comparison of stopover behaviour of species at localities at different stages of migration is probably difficult. It is proposed by some researchers that before barriers birds attain higher departure fat loads not by increasing their fuel deposition rate but probably by increasing their stopover duration (Schaub and Jenni 2001). If this is true, the proximity of Kuşcenneti National Park to Mediterrenean Sea and the Sahara might be one factor why adults have higher mean of stopover length than immatures.

4.6 Significance of Manyas Kuşcenneti National Park as a stopover site

The stopover habitat at Manyas Kuşcenneti National Park is a high quality one as revealed by high fuel deposition rates of retrapped birds. This habitat is probably utilised by different groups using different strategies to continue migration as was indicated by overall pattern of migration dynamics and as well of that of fat classes.

Populations of migratory birds are known to be limited not only by events at breeding or wintering grounds but also during migration and at stopover sites (Newton 2006). Links between breeding and nonbreeding areas is coined with the term "migratory connectivity" (Webster *et.al* 2002). Since Manyas Kuşcenneti National Park is situated at a critical location which probably is the last highly productive site before the crossing of two ecological barriers, it could mean that loss of this habitat will most likely affect the breeding populations further north.

There are very few studies suggesting high stopover site fidelity for migrant passerines although fidelity to high quality stopover sites and especially ones that are critically placed is expected (Catry *et. al* 2004). There were no controls (i.e. retrapping of individuals ringed in a previous season) between years in this study but the study period is too short to comment on stopover fidelity. Long term ringing at Manyas Kuşcenneti National Park could provide us with a clearer picture of stopover fidelity which would have an effect on conservation needs.

Although the site is already a protected area (National Park, Ramsar Site, A Diploma of European Council) there are still some damaging effects such as human-made changes in natural water levels leading to mass die-offs in willow trees. Moreover the strictly protected habitat is relatively small and suitable habitat elsewhere is subject to indiscriminate cutting and fires. The maintenance and improvement of such habitats at the national park should have high priority along with the more obvious objectives of waterbird protection and visitor management since their disappearance would impact tens of thousands of Willow Warblers from a wide area of breeding origin.

CHAPTER 5

CONCLUSION

Our results suggests that southern Marmara region in general, and Kuşcenneti National Park in particular, is crucial for stopover and refuelling of Willow Warblers during the autumn migration. The importance of the region is probably due to the fact that it provides the final biologically productive environment north of two important ecological barriers, the Mediterranean Sea and the Sahara.

The biometrical, phenology and body condition data strongly suggest that there are at least two, possibly more populations of Willow Warbler that pass through Kuşcenneti NP. These populations can belong to either different subspecies from widely separated regions of northern Eurasia or to populations with unique migratory strategies involving different route, timing and fueling parameters. The stopover data also sheds light on the preceding stages of migration of the birds that pass through. One group (dominated by T2 birds) could be migrating with shorter steps whereas a T5 dominated wave of migrants could be jumpers that prefer a nonstop strategy over longer distances.

Many small birds migrate through several legs of different duration, with periods of stopover among active migratory flight. Such stopovers where the bird replenishes fat stores and accumulates enough fat for the next leg of its journey is especially important right before a big ecological hurdle. For Willow Warblers in autumn migration, there is not one but two ecological barriers, the Mediterranean Sea and the Sahara, waiting ahead before reaching their wintering destination. Therefore, the presence, spacing and quality of suitable stopover habitats in Turkey are probably of critical importance.

Migrating Willow Warblers put on weight and fat within less than two weeks of stay at Kuşcenneti NP. The proportion of birds that gain weight/fat and the rate of this change indicate that the study site is a high quality stopover site for the species. The drier, less productive habitats further south in western and southern Turkey probably do not present many opportunities for other equally high-quality stopover sites. Therefore, it is quite possible that individuals that leave Kuşcenneti NP after fueling do not spend much time elsewhere and continue their migration over the Mediterranean and the Sahara.

This is the first systematical research on Willow Warbler migration and stopover ecology in Turkey, covering two consecutive autumn migration periods. Sample sizes are generally high when compared to similiar studies carried out in Europe, thus leading to safer interpretations. The findings shed light for the first time on stopover behaviour of Willow Warblers in Turkey and significantly contribute to our knowledge of the broader Black Sea/eastern Mediterranean basin. The study is especially valuable as there is still a gap of knowledge on stopover ecology of migrants before passage of large ecological barriers.

Willow Warbler is a long distant migrant which does not breed in Turkey. Yet with its highly utilized and irreplacable stopover sites, Turkey may provide a crucial ecological hub for this and other migrant passerines. Thus, these results point out to the need of international collaboration for conservation of especially long distance migrants whose migratory journey encompass large geographical areas of several countries.

Future research should try to make use of methods such as molecular phylogenetics or isotope ratio spectrometry in order to find the origin of populations involved as well as to accurately sex individuals captured. If the origins of different migratory waves are known, then their respective migratory strategies will be better understood and will guide us on focussing conservation effort on the right population and the right site.

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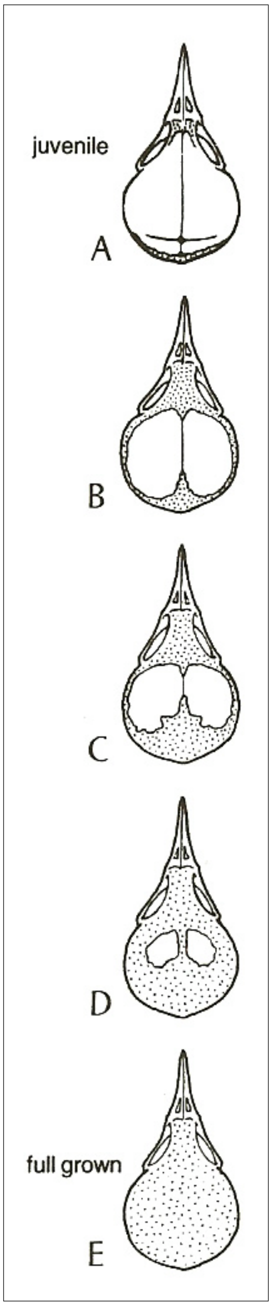
APPENDIX A

Key for skull ossification



It is considered safe to assume that all young passerines leave their nest before their skull is completely ossified (pneumatized). Initially the skull of a juvenile bird is made up of a single layer of a rather soft bone. Gradually this single layer becomes stronger (more ossified) while a second layer is developed on the inside. These layers are separated by an open space although bound together by numerous thin columns of bone. This phenomenon of gradual pneumatization of skull bone enables the aging of young birds so long as the process is not finished, whereas a fully ossified skull does not necessarily indicate an adult. The color of a unossified skull of a young bird is uniformly pinkish or reddish whereas that of an adult bird is whitish or pinkish-white and finely speckled with white dots formed by the ends of bony columns that binds two layers together. With some practice it is possible to distinguish between these two types of skull and it is fairly easy to identify a young bird if the demarcation line between single-layered and completely ossified parts of the skull is located (Busse 1984, Svensson 1992).

The skull ossification generally proceeds as shown in Figure A.1. The time span between A and E is normally three to six or seven months although it can be as little as two months in some species such as Willow Warbler (Svennson 1992). According to Jenni and Winkler (1994) skull pneumatization method for this species is useful only until the beginning of August although many first year birds show incomplete pneumatization until September.

Figure A.1 Stages of skull pneumatization.

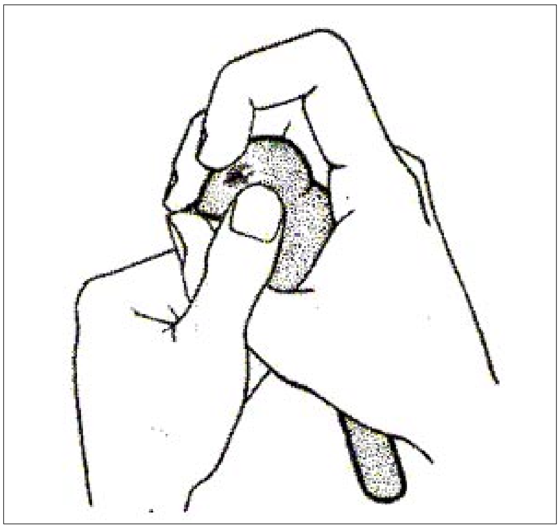


Figure A.2 Technique used for skull ossification examination.

The technique for examining the skull is as follows: The bird is held in one hand with head being fixed with thumb and a finger and bill lightly fixed between a finger and a thumb.Then the crown feathers of the bird is parted by a free finger for inspection either with a blow or wetting the skin with small amount of water (Figure A.2).

APPENDIX B

Key to the fat determination

(afterBusse 1983 and Kaiser 1993, combined) (Busse, 2000)

Determination of fat goes through three levels;

Level I- belly

Level II- furculum

Level III- pectoral muscles

I. 1) Belly is without visible fat or with reddish traces only- **IIA**

2) Belly with infused bands of fat (intestinum is visible..……………….............................**2**

3) Belly has a fused cover of fat; intestinum is not but the liver is visible…...................….**3**

4) Belly is completely covered with fat, a very narrow band of the liver may be visible but, if this is so, the roll of fat is just above it- **II B**

II A. 1)Air-sack is visible within furculum (some fat may ocur)……………….….............**0**

2) All the interior of furculum is covered with fat……………………........................**1**

II B. 1) Fat in furculum flat or concave…………………......……………..............................**4**

2) Fat in furculum forms a convex cushion- **III**

III. 1) Sides of pectoral muscles without stripes of fat………............……..........................**5**

2) Sides of pectoral muscles with stripes of fat………………………...........................**6**

3) Pectoral muscles partly covered with fat………......………………..............................**7**

.....4) Pectoral muscles completely covered with fat…...……………......................................**8**

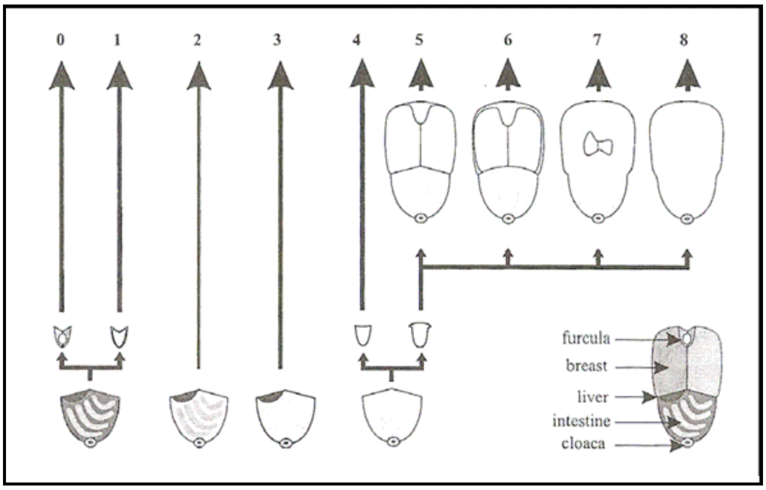
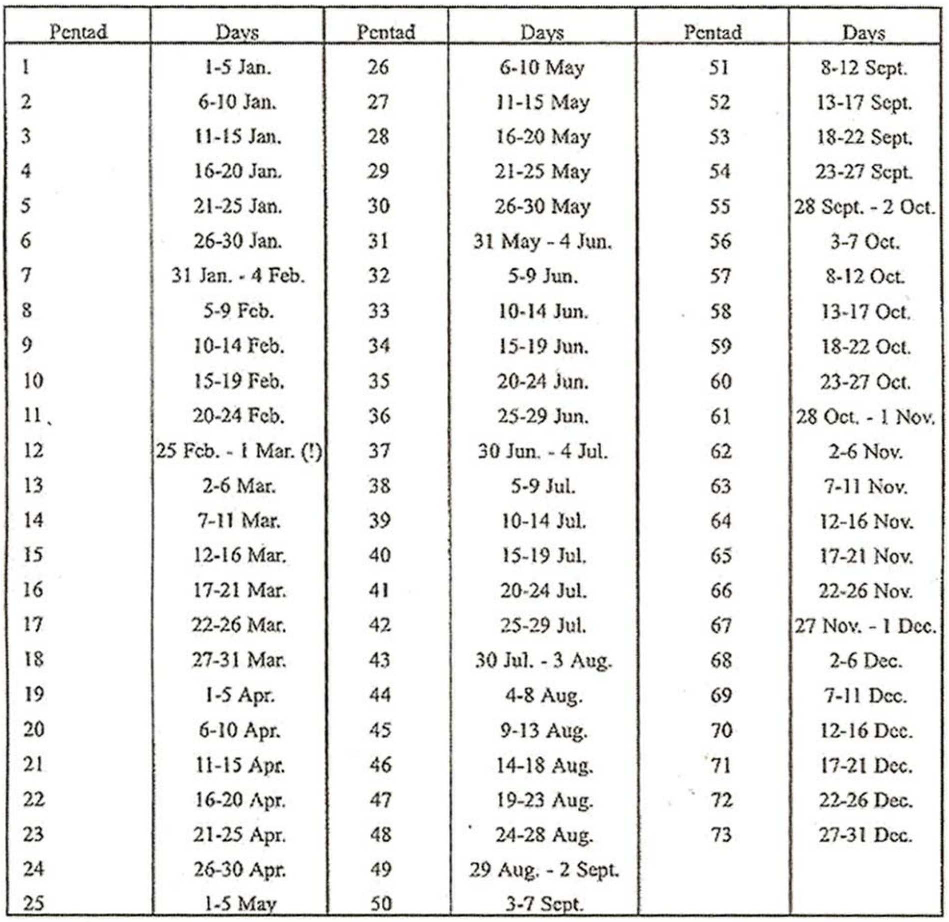


Figure B.1 Key to the fat determination

APPENDIX C

Pentades in full year system

Table C.1 The numbers of pentades in full year system (Busse 2000)



Pentad	Days	Pentad	Days	Pentad	Days
1	1-5 Jan.	26	6-10 May	51	8-12 Sept.
2	6-10 Jan.	27	11-15 May	52	13-17 Sept.
3	11-15 Jan.	28	16-20 May	53	18-22 Sept.
4	16-20 Jan.	29	21-25 May	54	23-27 Sept.
5	21-25 Jan.	30	26-30 May	55	28 Sept. - 2 Oct.
6	26-30 Jan.	31	31 May - 4 Jun.	56	3-7 Oct.
7	31 Jan. - 4 Feb.	32	5-9 Jun.	57	8-12 Oct.
8	5-9 Feb.	33	10-14 Jun.	58	13-17 Oct.
9	10-14 Feb.	34	15-19 Jun.	59	18-22 Oct.
10	15-19 Feb.	35	20-24 Jun.	60	23-27 Oct.
11	20-24 Feb.	36	25-29 Jun.	61	28 Oct. - 1 Nov.
12	25 Feb. - 1 Mar. (!)	37	30 Jun. - 4 Jul.	62	2-6 Nov.
13	2-6 Mar.	38	5-9 Jul.	63	7-11 Nov.
14	7-11 Mar.	39	10-14 Jul.	64	12-16 Nov.
15	12-16 Mar.	40	15-19 Jul.	65	17-21 Nov.
16	17-21 Mar.	41	20-24 Jul.	66	22-26 Nov.
17	22-26 Mar.	42	25-29 Jul.	67	27 Nov. - 1 Dec.
18	27-31 Mar.	43	30 Jul. - 3 Aug.	68	2-6 Dec.
19	1-5 Apr.	44	4-8 Aug.	69	7-11 Dec.
20	6-10 Apr.	45	9-13 Aug.	70	12-16 Dec.
21	11-15 Apr.	46	14-18 Aug.	71	17-21 Dec.
22	16-20 Apr.	47	19-23 Aug.	72	22-26 Dec.
23	21-25 Apr.	48	24-28 Aug.	73	27-31 Dec.
24	26-30 Apr.	49	29 Aug. - 2 Sept.		
25	1-5 May	50	3-7 Sept.		