

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

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ABSTRACT

Keşaplı Didrickson Ö., Didrickson J., Busse P. 2007. *Autumn migration dynamics, body mass, fat load and stopover behaviour of the Willow Warbler (Phylloscopus trochilus) at Manyas Kuşçenneti National Park (NW Turkey)*. Ring 29, 1-2: 67-89.

Turkey is located on one of the 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 the Willow Warbler, a passage migrant in Turkey, was documented and analysed at Manyas Kuşçenneti National Park (NW Turkey). Birds were mist-netted, 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 \pm SE) were 4.63 ± 0.06 and 3.84 ± 0.05 , while body mass reached 11.38 ± 0.07 and 10.37 ± 0.05 g for birds captured for the first time. Fat scores in 2003 showed a bimodal distribution with peaks of T_2 and T_3 , indicating populations or groups with different migratory strategies. The number of retraps constituted 9.2-12.1% of birds captured. In both years, minimum stopover length ranged from 1 to 15 or 16 days with a median of 5 days (averages 5.26 and 5.54, respectively). 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 had arrived. In this second study documenting the Willow Warbler migration in Turkey, it was revealed that such wetlands as Manyas Kuşçenneti National Park provide crucial stopover habitat for possibly several populations of the species enabling them to gain necessary fat loads before crossing two major ecological barriers, the Mediterranean Sea and the Sahara.

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Key words: *Phylloscopus trochilus*, Willow Warbler, migration, stopover behaviour, fat load, Western Turkey

INTRODUCTION

Storage of extensive fat reserves by migratory birds prior to flight is one of the main adaptations needed for migration, particularly in the case of a long-distance migrant (Lack 1968, Berthold 1993, Åkesson and Hedenström 2007). Compared to the carbohydrates and proteins, the lipids are the most energy efficient molecules that birds could store (Berthold 1993, Ścisłowska and Busse 2005). Moreover, their storage does not require extra water. Therefore fat is an optimal flight fuel for migrants whose target during migration is to put on as much energetic fuel stores as possible without becoming too heavy (Alerstam 1990).

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, which means 60-100% of the fat-free body mass (Berthold 1993). The amount of fat reserves found in a migrant's body is known to be related to the migratory distance to be covered, associated ecological conditions, the stages of migration and thus is of paramount importance when investigating the migratory strategies of migrants (Berthold 1993).

Especially for a small passerine, the vast distances to be covered during migration necessitates refuelling (Alerstam 1990). Therefore, a typical migratory journey 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 site and replenish their fat reserves to make next stages of flight. Birds are known to spend more time and energy on stopover than flight during the migration (Alerstam and Hedenström 1998, Schaub *et al.* 2001). Hedenström and Alerstam (1997) give 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 investigations are limited for most species. Many studies on the stopover ecology were carried out for several species, *e.g.* the Reed Warbler (*Acrocephalus scirpaceus*), but research on the stopover behaviour immediately before and after crossing barriers is very rare although such sites are probably of profound importance for the success of migration (Yosef and Chernetsov 2005). The stopover duration and the fuel deposition rate are crucial factors shaping migration strategies of birds (Alerstam and Hedenström 1998). 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).

Stopping over several times and putting on small amounts of fat at each migratory step is more energy efficient since the transport economy of high fat loads is poor. However, during migration birds are faced with ecological barriers like

oceans, glaciers, deserts where they cannot stop and replenish their fat reserves (Alerstam 1990). Migratory birds within the European-African migration system face two major ecological barriers, the Mediterranean Sea and the Sahara, both of which offer very few opportunities 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 Mediterranean in an extensive non-stop flight of some 30-40 h. 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 south-western and south-eastern 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 refuelling, but possibly with stops (Bruderer and Liechti 1999).

Although Willow Warbler is a common passage migrant in Turkey during both spring and autumn migrations (Porter 1983, Keşaplı Can and Keşaplı Didrickson 2003, Keşaplı Can *et al.* 2004), this is the first detailed study of the species in Turkey. The aims of this study are to find out the autumn migration dynamics (phenology) of Willow Warblers at Manyas Kuşçenneti National Park and to record and analyse changes in body mass, fat load and stopover duration between years and between age and sex groups.

STUDY AREA

The data analysed in this study were collected during a larger scale ringing study carried out in spring and autumn 2002 and 2003 at 2 sub-stations around Lake Manyas (Kuş), south of the Marmara Sea in north-western Turkey (Fig. 1). The main sub-station for autumn ringing was Manyas Kuşçenneti National Park (40°14'N, 28°02'E, 16 m a.s.l.), which is situated by the north-eastern coast of Lake Manyas. Some data used in this study were also collected at Soltra sub-station which is located approximately 3 km south-east from Manyas Kuşçenneti National Park.

Lake Manyas (15 700 ha) is a shallow eutrophic freshwater lake with an average depth of 3 m. Manyas Kuşçenneti National Park (64 ha) is located at the delta formed in the place where Sığircı stream enters the lake (Yarar and Magnin 1997). The habitat of the National Park is dominated mainly by seasonally flooded willow forest (*Salix alba*, *S. caprea* and *S. excelsa*) and dense reedbeds (*Phragmites australis*, *Typha angustifolia*) fringing the lake. Common White Waterlily (*Nymphaea alba*) and Sanicle-leaved Water Crowfoot (*Ranunculus saniculifolius*) can be found near or within the reedbeds. Beside willows, several other trees are present at the park area including ash-trees (*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 contribute

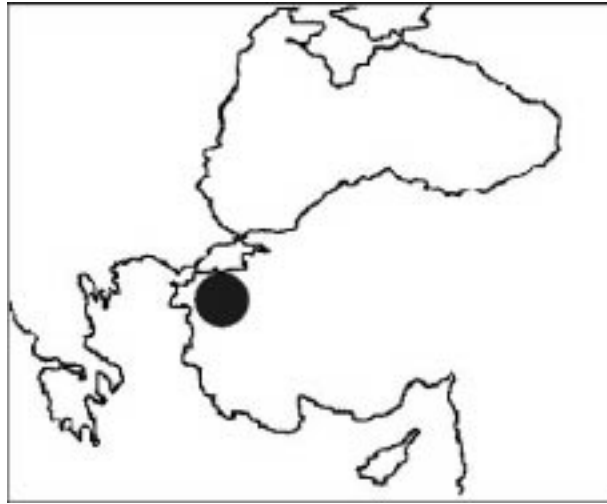


Fig. 1. Localization of the study area on a map of Turkey

to the richness of habitats for birds, having different plantations each season. During this study there were extensive sunflower (*Helianthus annuus*) plantations. Soltra was a few hectares oak (*Quercus spp.*) loose growth surrounded by cotton fields and empty resting fields.

MATERIAL AND METHODS

This study focuses on autumn migration data of Willow Warblers captured at Manyas Kuşçenneti National Park and Soltra sub-stations in 2002 and 2003. In 2002, the ringing study was carried out in Soltra sub-station between 16 August and 12 September, the date after which the sub-station was finally closed due to very low migration activity. On 14 September the study was moved to Manyas Kuşçenneti National Park and continued until 22 October. In 2003, the ringing was carried out only at Manyas Kuşçenneti National Park between 26 August and 19 October.

Methodology was based on capturing, ringing, aging and obtaining physiological and biometrical data of Willow Warblers. The birds were fat scored visually based on a 3-level (furculum, belly and pectoral muscles) inspection key according to a 9-graded scale (after Busse 1983 and Kaiser 1993, combined, Busse 2000). The study was continuous throughout the day and the study period with nets being open 24 hours a day in good weather conditions. The mist-netting and handling routine followed the guidelines of SEEN (Busse 2000). Capture statistics are given in Table 1.

The birds were sexed *post factum* on the basis of wing length distribution. The wing length of all captured Willow Warblers ranged from 60 to 75 mm. 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). 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 could be allocated to either sex.

Table 1
Number of birds ringed and retrapped in 2002 and 2003

Study period	Ringed	Retrapped	% retrapped
16 Aug. – 21 Oct. 2002	543	50	9.21
26 Aug. – 19 Oct. 2003	929	112	12.06
Total	1472	162	11.00

The wing length distribution of Willow Warblers was analysed (Fig. 2). Based on the two discernible peaks in wing length frequency graphs, which were assumed to represent different sex classes, and the available literature (Cramp 1992, Svensson 1992) the following sex allocation criteria were adopted:

Adults with wings 67 mm were assumed to be females, with wings 69 mm – males (birds with wing length 68 mm were excluded from the analysis),

Immatures with wings 65 mm were assumed to be females, with wings 67 mm – males (birds with wing length 66 mm were excluded from the analysis).

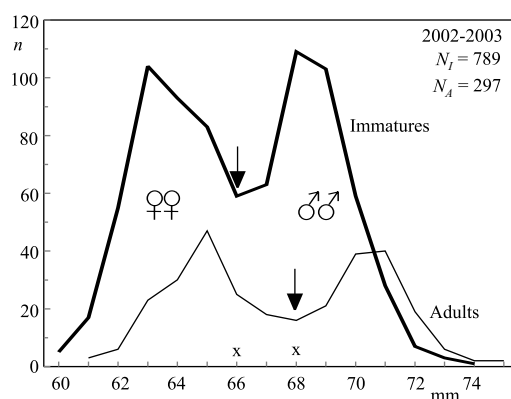


Fig. 2. The distributions of the wing length of immatures and adults for the birds caught in 2002-2003 as the base for sex discrimination. Arrows point at assumed borders between sexes. Individuals with wing lengths pointed as x-es were not classified

Only 61.9% and 72.2% of all captured birds could be allocated to either sex in 2002 and 2003, respectively. In 2002 the number of females was 169 and the number of males – 168; in 2003 these numbers reached 340 and 336, respectively. Thus for both years the sex ratio was roughly 1 : 1.

According to this method of sexing some birds could have been placed in wrong sex classes, therefore leading to misinterpretation 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 could be 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 uncertain sex, reduces the probability of such mistakes.

Results were analysed (including basic statistical tests) using custom built ringing analysis software PODAB (version 7.0) as well as spreadsheets. In order to remove excessive variation within raw data and to have a more clear presentation, smoothing based on weighted running averages was used on many graphs (Busse 2000). 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 – number of birds ringed on the x^{th} day.

For the purpose of analysing fat load change over time by change in grams rather than change in classes, weight standardization was adopted as a method after Busse (1970). Standardized 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 T_2 . As a result, the standardized weight of each bird in the sample is calculated as the weight that the bird would have if it had a fat score of T_2 . PODAB automatically calculates average fat load in grams based on standard weight, using the formula below:

$$t_g = \frac{(n_i - c_i)}{N}$$

where:

n_i – number of individuals,

c_i – correction for a particular fat class,

N – total number of individuals in the group,

t_g – fat in grams for that group.

RESULTS

Total phenology

The general phenology graph for 2002 reveals a single obvious peak towards the end of the season, whereas in 2003 three peaks are discernible (Fig. 3).

For 2003 the relationship between migration dynamics of birds that stopped over (retrapped) and birds that were only captured once during the migration season (never retrapped) was investigated. The majority of the retrapped birds were captured initially in the middle of the migration season, whereas the never retrapped birds came in several waves starting from the beginning of the migration season (Fig. 4). The first peak of the total migration dynamics was made up mostly

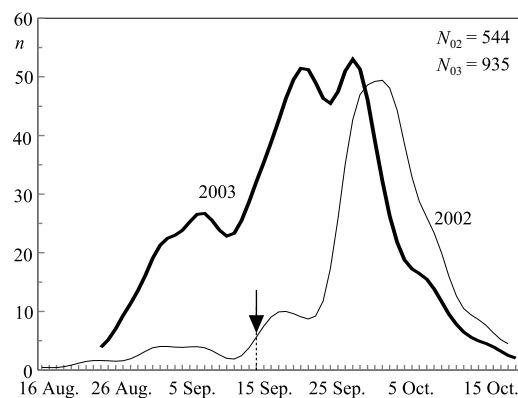


Fig. 3. Total seasonal dynamics in 2002 and 2003 (smoothed by a running average). Arrow shows the date of changing catching locality in 2002.

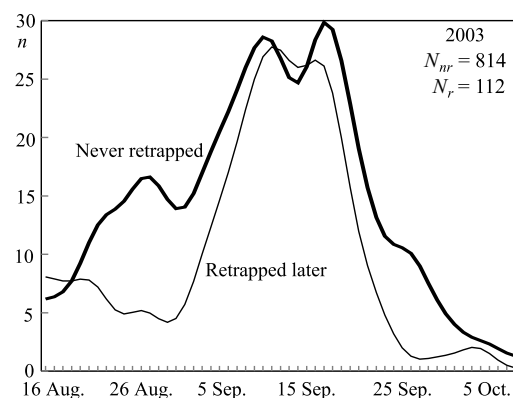


Fig. 4. Total seasonal dynamics of retrapped and never retrapped birds in 2003 (smoothed)

of the never retrapped birds, while the first of the latter two more intensive peaks were made up mostly of the birds that stayed longer, thus were retrapped. The last peak of the total seasonal dynamics seems to comprise peaks of both bird groups.

Migration of sexes

The total seasonal dynamics was checked for any sexual differentiation. This analysis was carried out only for 2003, since sample size was larger for that year. As is clear in Figure 5, there is no obvious differentiation in migration dynamics of sexes in 2003.

Migration of age groups

In 2002 the migration of immatures and adults peaked on 27 September and 2 October, respectively. Similarly, there was a 5-day difference between the median

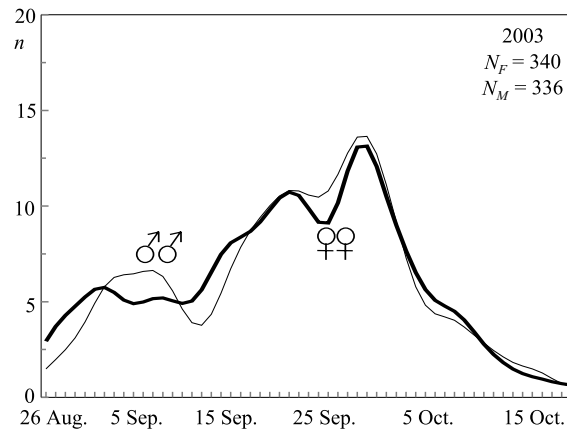


Fig. 5. Total seasonal dynamics of males and females in 2003 (smoothed)

dates of passage for age groups in 2002 with immatures earlier than adults. In 2003, the migration of adults and immatures peaked on 17 and 27 September, respectively, whereas the median days of passage for age groups were the same.

As for age specific differences throughout the study period the cumulative passage data for each year and age groups were analysed (Fig. 6). In 2002 until around mid-September, adult and immature passages were synchronised, although afterwards there was a heavier passage of immatures. The passage of age groups became synchronised again towards the end of the study period. In 2003, however, the passage was unsynchronised till the third week of September with a heavier passage of immatures. The passage of age groups after this period was in synchrony till the end of the study period as is also shown by median dates of passage. Generally, it seems that immatures migrated a little bit earlier.

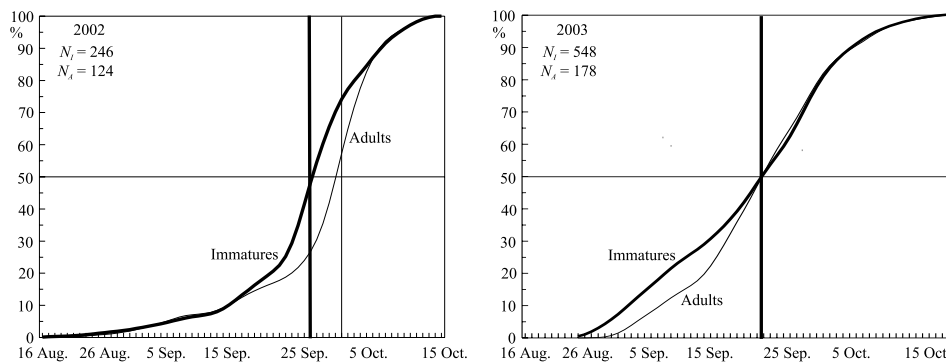


Fig. 6. Total seasonal dynamics of adults and immatures in 2002 and 2003 (shown as daily cumulative percentage). The vertical lines mark the median dates of passage.

Migration of fat score groups

In 2002 the distribution of fat scores was unimodal with the mode at T_3 , while in 2003 it was clearly bimodal with modes at T_2 and T_3 . Distributions of body mass values were differentiated too. Figure 7 shows a differentiation in migration phenology in 2003 of two fat classes T_2 and T_3 with a clearly heavier passage of T_3 for most of the study period, except for a period between 15 and 25 September, which corresponds to the second migration peak in total phenology. The ratio of T_3 to T_2 birds showed significant changes over time, with an excess of T_2 birds at the middle of the migration season around late September, and an excess of T_3 birds before and after.

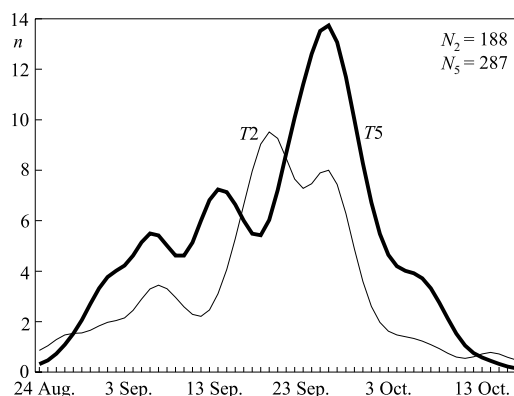


Fig. 7. Total seasonal dynamics of fat classes T_2 and T_3 in 2003 (smoothed)

Stopover behaviour

Stopover length

The number of birds that were retrapped was 50 and 112 for 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 with the median stopover length 5 days. For 2003, the distribution of stopover length of retrapped birds was also analysed. The majority of birds stayed five days or less with maximum number of birds ($n = 20$) staying for only 2 days. The maximum number of days of stay, however, was 16 days, although only 6 birds stayed more than 11 days. Here, there is a very interesting pattern of retrapped birds with a very regular three-day periodicity of recapture (Fig. 8).

In the case of retraps, the stopover length for each fat score was also analysed (Table 2). For both years, T_3 birds had the longest stopover, whereas birds with lower fat scores stopped over for a shorter time than T_3 birds. Altogether, birds with fat scores T_0 - T_2 stayed for 6.3 days on average ($n = 51$) with median of 6 days, while T_3 birds stayed for as long as 8.8 days ($n = 16$) with median being 9 days. The stopo-

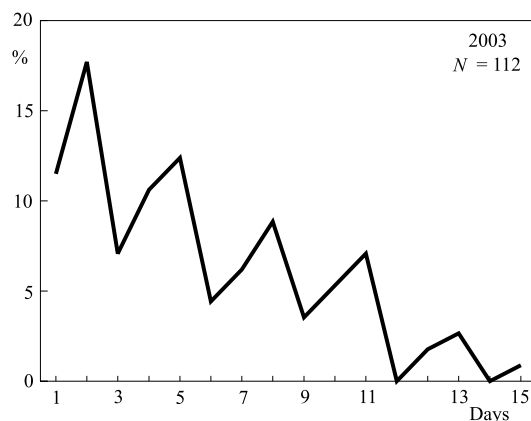


Fig. 8. Distribution of stopover lengths in 2003 (shown as raw data)

ver length is the lowest for higher fat scores T_4 - T_6 with mean length of stay 4.4 days ($n = 90$) and median – 3.5 days. These significant differences are difficult to explain at the moment.

Table 2
Stopover length by fat score

Retraps stay (days)		Fat score						
		0	1	2	3	4	5	6
2002	Avg.	6.4			7.6	6.4	4.3	3.6
	SD	3.7			2.9	3.5	3.9	2.9
	N	8			5	10	18	9
2003	Avg.	7.4	5.4	6.1	9.3	5.1	3.9	3.1
	SD	3.6	4.2	3.3	4.8	3.6	2.8	1.6
	N	8	5	30	11	17	28	8

Body mass and fat

For 2002 and 2003, the mean body mass on arrival was 11.38 g and 10.37 g, and the mean fat score was 4.63 and 3.85, respectively (distributions are presented in Figure 9). The differences between years for body mass and fat scores are highly significant (unpaired t -test: $p < 0.001$). In 2002 the majority of birds on first capture belonged to T_5 and above (67.6%), whereas for 2003 this proportion was only 45.5%.

The changes of fat classes over time were also analysed for both studied years (Fig. 10). For 2002, birds with lower fat classes seem to dominate the first few weeks, *i.e.* the time of ringing at Soltra sub-station, where the ringing totals were low, as is clear also from large standard error. In both years, birds with highest fat load were recorded in the second half of the migration period, except for the last days of migration in 2003.

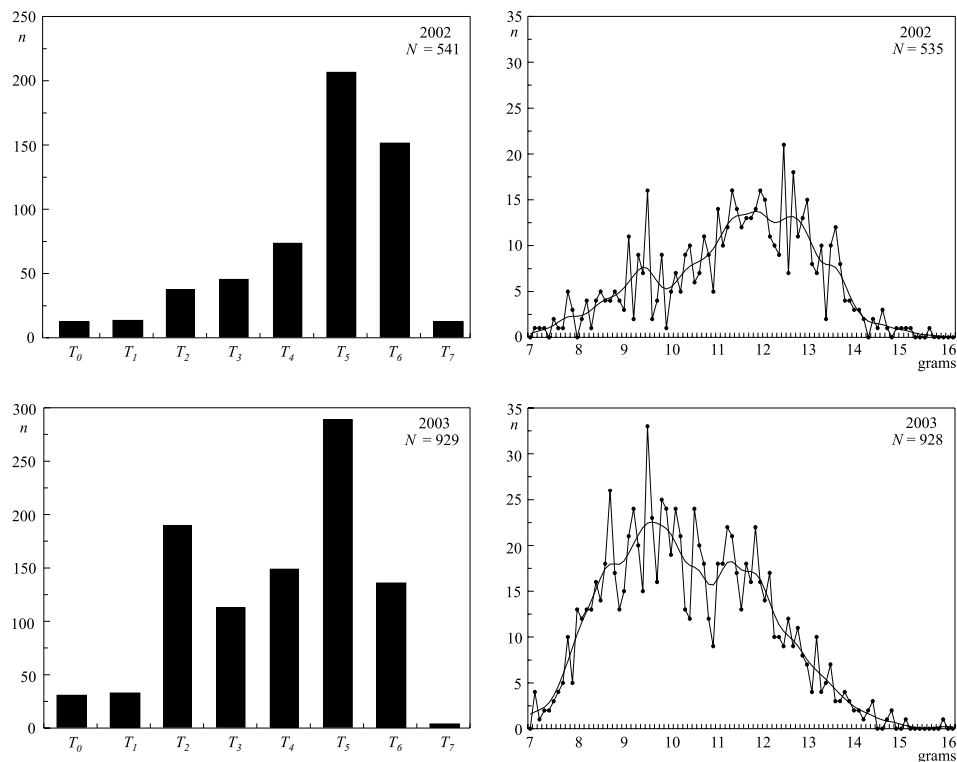


Fig. 9. The distribution of fat classes (left panels) and actual body mass (right panels) in 2002 and 2003. On body mass panels: dots – variation of the raw data (by 0.1 g) and line – smoothed data.

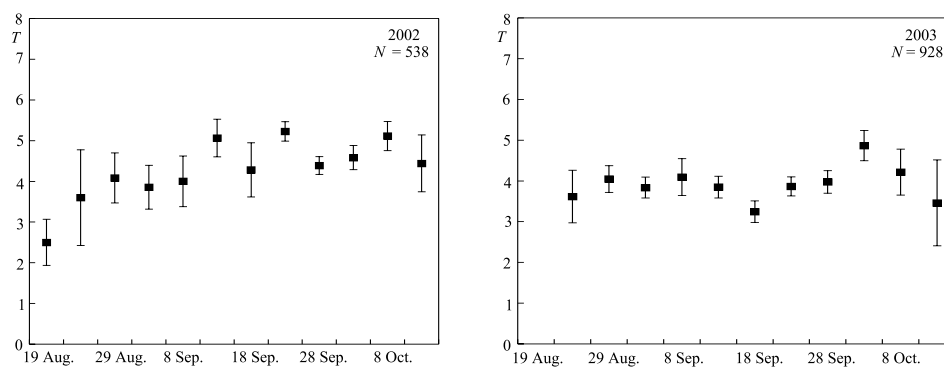


Fig. 10. Fat class change over time in 2002 (left) and 2003 (right). Mean values and $SE \times 1.96$ for 5-day period are given

For 2003, age and sex differences of body mass and fat score were also investigated (Table 3). Both adult and immature females were found to be fatter than males during most of the migration period, except for immature males being fatter

than females in the last week of August and adults being of nearly equal fatness in the first half of the season (Fig. 11). Adult males were about 8.5% heavier but had an average fat score that was 87% of that of adult females. Similarly, immature males were 7.5% heavier but carried 89% of the fat load of an average immature female. To sum up, although males of any age were heavier (*i.e.* larger), their fat loads were lower.

Table 3
Body mass and fat score of birds according to age and sex groups

	<i>N</i>	Mean \pm SE (<i>SD</i>)	
		Body mass (g)	Fat score (0-8)
2002 (all)	544	11.38 \pm 0.07 (1.63)	4.63 \pm 0.06 (1.47)
Adults	124	11.39 \pm 0.14 (1.57)	4.61 \pm 0.14 (1.52)
Immatures	246	11.45 \pm 0.11 (1.70)	4.67 \pm 0.09 (1.43)
Adult females	61	10.80 \pm 0.18 (1.40)	4.63 \pm 0.21 (1.615)
Adult males	52	11.97 \pm 0.20 (1.47)	4.58 \pm 0.18 (1.33)
Immature females	108	10.90 \pm 0.16 (1.60)	4.65 \pm 0.15 (1.60)
Immature males	116	11.95 \pm 0.16 (1.66)	4.70 \pm 0.12 (1.31)
2003 (all)	935	10.37 \pm 0.05 (1.61)	3.85 \pm 0.05 (1.62)
Adults	178	10.54 \pm 0.12 (1.62)	4.08 \pm 0.12 (1.62)
Immatures	548	10.25 \pm 0.07 (1.61)	3.75 \pm 0.07 (1.62)
Adult females	91	10.14 \pm 0.16 (1.50)	4.34 \pm 0.17 (1.62)
Adult males	77	11.01 \pm 0.19 (1.64)	3.81 \pm 0.18 (1.56)
Immature females	249	9.84 \pm 0.10 (1.52)	3.96 \pm 0.10 (1.60)
Immature males	257	10.60 \pm 0.10 (1.54)	3.53 \pm 0.10 (1.60)

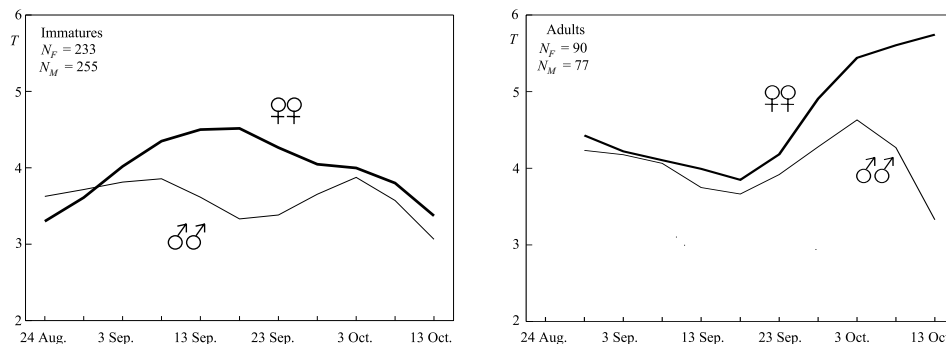


Fig. 11. Fat class change over time for sexes; immatures (left panel) and adults (right panel) in 2003

The results showed that both in 2002 and 2003 the mean body mass on first and last captures significantly increased by 9.5% and 16.8%, respectively. Similarly, average fat class values increased by 25.5% and 42.5%, respectively (Table 4). In both

years, retrapped birds increased between their first and last captures both their body mass and fat score but mean fattening rates did not differ between years (unpaired *t*-test: $p = 0.178$). The detailed stopover pattern for each fat score is given in Figure 12.

Table 4
Body mass and fat score of retrapped birds – mean \pm SE (SD)

	<i>N</i>	Body mass		Fat score	
		First catch	Last catch	First catch	Last catch
2002	50	10.81 \pm 0.20 (1.36)	11.84 \pm 0.17 (1.22)	4.24 \pm 0.21 (1.46)	5.32 \pm 0.13 (0.94)
2003	112	9.87 \pm 0.14 (1.49)	11.53 \pm 0.15 (1.58)	3.32 \pm 0.16 (1.72)	4.73 \pm 0.14 (1.47)

Changes in body fat were also compared through calculating standardized weights. Figure 13 shows the pattern of body mass and fat load change (in grams) following initial capture of retrapped individuals. The birds were losing fat and, slightly, body mass for up to 2-3 days after first capture but then they started to put on weight in an increasing rate until the ninth or tenth day after first capture. Fat load change in grams was the highest when the stopover length was 10 days.

Age specific differences in stopover behaviour

The age specific differences in stopover behaviour of retrapped Willow Warblers in 2003 was analysed. The stopover range was found to be similar for both age groups: adults – 1-14 (median 5 days) and immatures – 1-16 days (the same median). Although the median stopover length for age groups were the same, the adults on average stayed longer than the immatures: 6.2 days ($N = 16$) vs 5.5 days ($N = 77$).

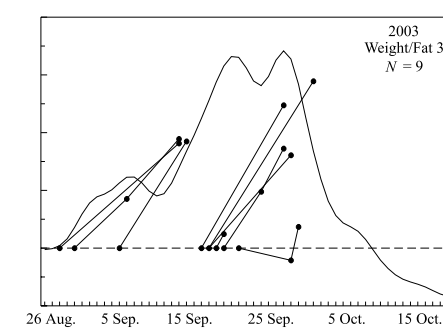
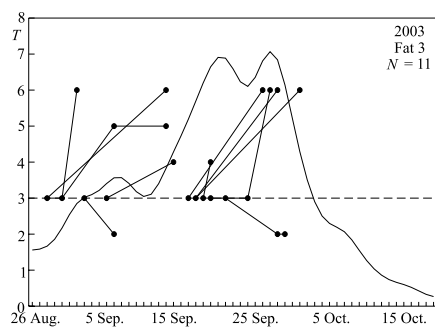
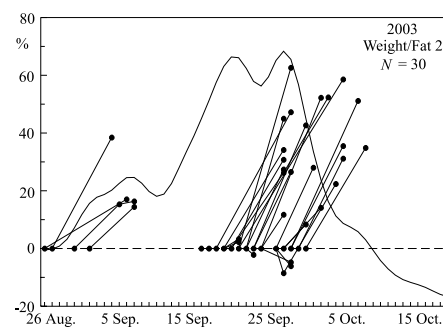
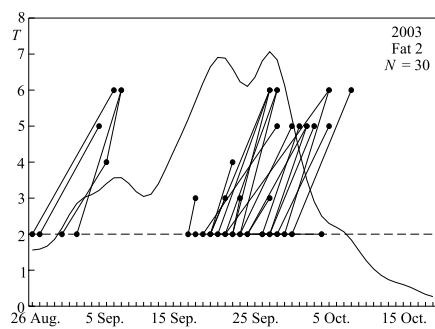
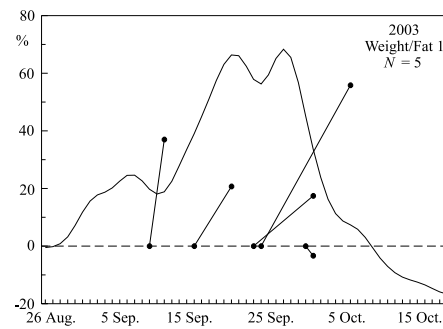
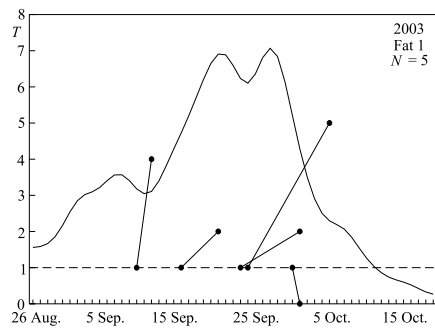
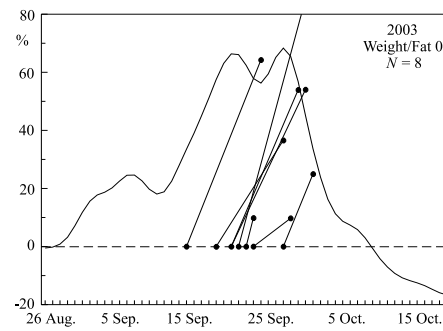
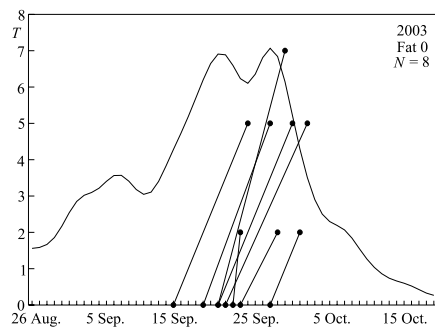
The mean increase in actual body mass of adults and immatures was 17.9% and 12.8%, respectively (Table 5). The mean body weight increase per stopover day was 0.30 g for adults and 0.23 g for immatures. This means that the adults put on fat (and weight) during stopover at a faster rate than did the immatures.

Table 5
Mean body mass and fat score change of retrapped birds in 2003 according to age groups

	<i>N</i>	Fat score change	Body mass change (%)	Average gain (g)
Adults	16	+1.88	+17.9	+2.87
Immatures	77	+1.28	+12.8	+2.32

DISCUSSION

The results of this study show that Willow Warblers migrate through Manyas Kuşçenneti National Park from mid-August to end of October. Passage seems to be most intense from early September to early October (Fig. 3). However, since this



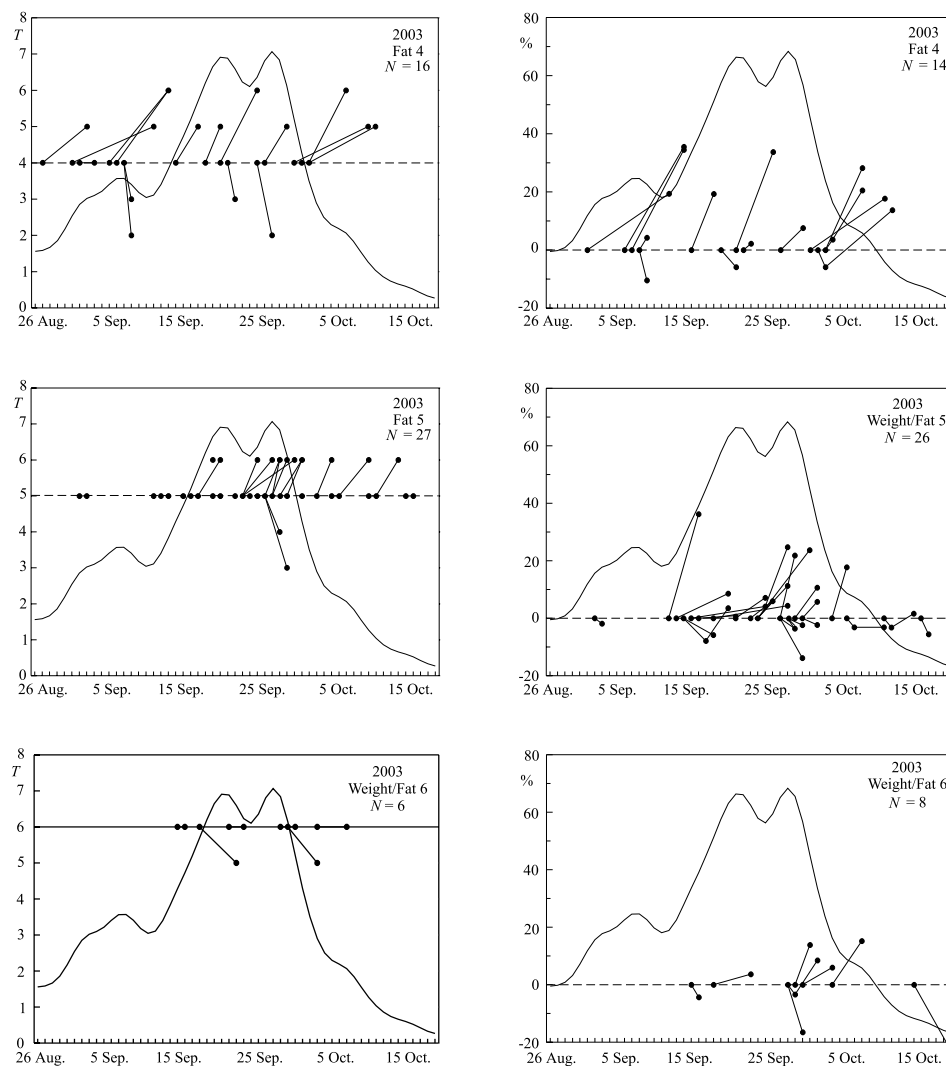


Fig. 12. Individual changes of fat score (left panels) and body mass (right panels) of retrapped individuals grouped according to initial fat score. Horizontal broken lines show initial fat and body mass levels. The background line – total catching dynamics

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 generally 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 the Willow Warbler as the commonest migrant on many days between 6 August and early September with the latest individual observed as late as on 29 October. This additionally emphasizes that in future

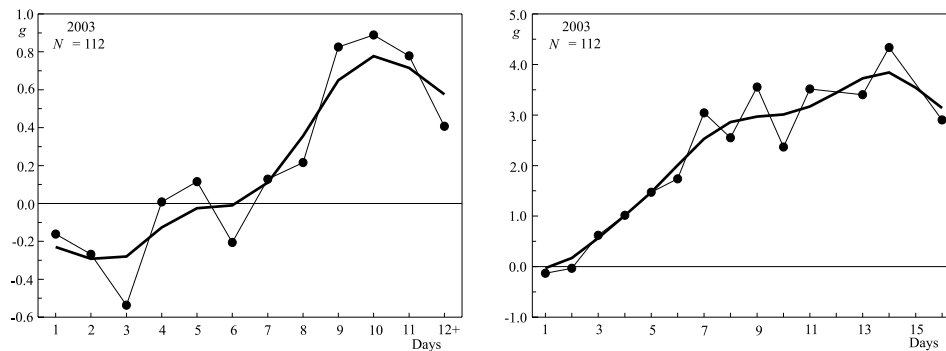


Fig. 13. Fat load (left) and actual body mass (right) changes in grams of retrapped birds in 2003 (raw and smoothed curves)

studies, the fieldwork should ideally start at the beginning of August in order to have a full picture of Willow Warblers using Manyas Kuşçenneti National Park as a stopover site. The high numbers of birds captured is in accordance with literature, which states that the species is abundant in eastern Mediterranean in autumn (Cramp 1992). The peaks in general phenology graphs for 2002 and 2003 possibly correspond to separate migration waves that could represent different populations with separate migration strategies, especially observed as a difference in timing of migration. The low catch numbers in the beginning of the 2002 migration period result from the location of catching in worse habitat in Soltra sub-station.

The phenology graphs for retrapped and never retrapped birds in 2003 (Fig. 4) suggest that birds that were not retrapped predominate in the earlier captures, whereas birds that arrive later stopover (become retrapped). The first migration wave in 2003 is probably made up of birds that might have interrupted their migratory journey only for a short time due to weather conditions. If these birds are from populations that prefer to migrate with longer steps, this can be the reason why these birds were not retrapped. They probably departed as soon as the weather improved.

In this study the data for 2003 was analysed for sex groups and no obvious differentiation in migration dynamics was found (Fig. 5). 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 for this study 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).

The cumulative passage graphs for different age groups (Fig. 6) 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 synchronised passage of age groups until mid-September is difficult to interpret due to a low sample size ($n = 41$) during that period. In 2003 the passage of immature birds is heavier until around the third week of September, 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 progresses 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.

The phenology of T_2 and T_3 birds in 2003 show significant changes over time, with an excess of T_2 birds in the middle of the migration season around late September, and an excess of T_3 birds before and after (Fig. 7). These changes may represent particular waves of migratory populations that have different mean fat loads because they have separate migration strategies. The low number of T_2 birds in 2002 could also support this timing difference if we could better understand the reason of the late total passage in 2002 compared to 2003. If it was mainly caused by later passage of heavier birds (*i.e.* T_3) then low number of T_2 birds in 2002 could be explained by a late start of the study at the National Park. However, it is not possible with available data to safely comment about the lack of T_2 wave in 2002, which should ideally be further investigated.

The analysis of stopover behaviour reveals very similar minimum stopover duration range and exactly the same median stopover length for both years. This might suggest that the Kuşçenneti National Park habitat has been similar between these years for the Willow Warblers that stopover there and exploit it. It could also mean that the stopover behaviour of the Willow Warblers passing through Kuşçenneti National Park in these years are similar, which in turn implies that the composition of birds, as far as different body condition, age/sex groups and populations are concerned, are fairly stable.

When the relationship between stopover length and fat classes was investigated, a rather strange phenomenon was revealed with T_3 birds stopping over the longest and both higher and lower fat classes staying shorter (Table 2). It is expected that birds with the lowest fat loads will stay the longest and replenish depleted fat reserves provided that the locality is a resourceful one. Birds that land with already high fat load stay shorter as they have to add only a little fat to reach an optimal fat load.

The distribution of stopover length of birds that were retrapped in 2003 shows also a peculiar pattern (Fig. 8). 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 the Redstart (*Phoenicurus phoenicurus*), where the pattern was exactly the same as for the Willow Warbler here (Busse 1972). This is a secondary problem in this paper, but it seems to be an interesting challenge for further studies of physiological and/or behavioural aspects of stopping over.

There are several studies investigating age specific differences in stopover behaviour, e.g. 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). Our results show that at least in 2003 adults put on fat load and weight at a faster rate than immatures (Table 5). The mean stopover length of adults was found to be higher than that of immatures in 2003. In one study which took place in Morocco the stopover length of immature Reed Warblers (*Acrocephalus scirpaceus*) was found to be larger than that of adults (Rguibi-Idrissi *et al.* 2003). Similarly, in a study in New Mexico (USA) immature Wilson's Warblers (*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, particularly by the distance from ecological barriers. Therefore, a comparison of stopover behaviour of species at localities at different stages of migration is 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 Kuşçenneti National Park to the Mediterranean Sea and the Sahara might be one factor why the adults have longer mean stopover duration than the immatures.

The mean values of body mass and fat of Willow Warblers that pass through the area in 2002 and 2003 is clearly different. These differences could be either due to different composition of individuals from different populations with separate migration strategies passing through Kuşçenneti in 2002 and 2003, or different physiological states of the same populations that were passing through. In one study that looked at the migratory state of several long-distance migrants during autumn migration in north-eastern Bulgaria the mean values of body mass and fat class for Willow Warblers in 2002 were similarly larger than those in 2003 (Ilieva and Zeht-indjiev 2005). However, in this study these two years should be compared with caution since in 2002 the fieldwork started at Manyas Kuşçenneti National Park substation only from mid-September – 18 days later than in 2003. Therefore, the shorter period of ringing activity at the beginning of ringing in the park in 2002 meant lower retrapping possibilities, although two birds that had been ringed in Soltra in 2002 were retrapped in the National Park 7 and 14 days later. Probably, the birds that land in Soltra quickly disperse to the more suitable stopover habitats in the vicinity, such as the National Park. Therefore, 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 of time and gained fat. Thus, 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.

For both 2002 and 2003 the detailed pattern of stopover clearly shows that the birds that stopover at Manyas Kuşçenneti National Park successfully replenish their reserves for the next step of their autumn migration. It is obvious from the graphs that show changes in fat class and weight for each bird of each fat class in 2003 (Fig. 12) that birds which arrive with lower fat classes experience a significant change particularly in fat class, although the birds that arrive with already high fat scores (*i.e.* T_5 , T_6) do not experience so pronounced change. However, if the peaks of low and high fat classes (T_2 and T_5) do indeed show groups 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 intermittent 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 the desert (Biebach 1990, Berthold 1993). Additionally, the difference between classes is 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. These findings suggest that most Willow Warblers that stopped over at Manyas Kuşçenneti 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-distance migrants is quite dynamic over a short span of time (hours or days), and birds can store and use both lean mass and fat mass during migration (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 pre-migration 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 (Fig. 13) it is not reflected in fat load change in grams since the gain may be converted into organ size enlargement.

The Willow Warbler is known to have a fast refuelling capacity (Cramp 1992). In a study of autumn migration on the western coast of Portugal, the 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, in this study, for 2003 the results yielded a significantly positive (average 1.5 g; $p < 0.001$) rate of fattening for birds with a median stopover length of 5 days. Furthermore, the retrapped birds continued to put on weight for the first two weeks of their stay. Body mass change was the highest when the birds stopped for 14 days. Overall, both in 2002 and 2003 the majority of the birds that stopped over put on a significant amount of fat.

There is evidence that migrating Willow Warblers put on little weight and/or fat in the early stages of their migration in northern latitudes. Average body mass values for populations of Willow Warblers on autumn migration are found to vary between 8.2 and 8.8 g in Ottenby (Sweden), in Helgoland (Germany) and Bukowo (Poland), whereas birds captured in locations that are just before an ecological barrier are heavier and fatter, *e.g.* 10.9 g at Karpathos island, Greece (Ilieva and Zeht-indjiev 2005). The departure body mass of birds retrapped in Malta is also high in autumn (Sultana and Gauci 1986). Similarly, individuals captured at Manyas Kuşçenneti National Park – when compared to birds captured further north – were heavier and fatter, with arrival body mass values being 11.38 g and 10.37 g in 2002 and 2003, respectively. The departure weights of the retraps further reveal the 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 and Bilgin 2005). Willow Warblers that stopped at METU were significantly fatter than Willow Warblers that stopped at Manyas Kuşçenneti National Park as reflected by much lower percentage of birds with fat score T_6 and above (29.6% in 2002 and 14.5 % in 2003) in the latter place.

Populations of migratory birds are known to be limited not only by events on breeding or wintering grounds but also during migration and at stopover sites (Newton 2006). The Willow Warbler is a long-distance migrant that does not breed in Turkey. Yet with its highly utilized and irreplaceable stopover sites, Turkey may provide a crucial ecological hub for this and other migrant passerines. Accordingly, our results strongly indicate that Manyas Kuşçenneti National Park is possibly used by different populations for essential fuelling before barriers crossing. Moreover, since it is known that birds could show fidelity to high quality stopover sites, the monitoring of Manyas Kuşçenneti National Park habitat is likely to be crucial for conservation of several populations of the Willow Warbler. Since Manyas Kuşçenneti 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.

CONCLUSIONS

Our results on the phenology and body condition data strongly suggest that there are at least two, possibly more, populations of the Willow Warbler that pass through Kuşçenneti NP. These populations can belong to populations with unique migratory strategies involving different route, timing and fuelling parameters. The stopover data also shed light on the preceding stages of migration of the birds that pass through. One group (dominated by T_2 birds) could be migrating with shorter steps, whereas a T_5 dominated wave of migrants could be "jumpers" that prefer a non-stop strategy over longer distances.

Long-term standardized ringing and additional field methods (e.g. orientation experiments, isotope ratio spectrometry, molecular phylogenetics) are required in order to better understand the origin and thus migration strategies of these populations, as well as to accurately sex the individuals captured.

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