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Stopover characteristics of Sedge Warblers (*Acrocephalus schoenobaenus*) in central Iberia

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The Sedge Warbler (*Acrocephalus schoenobaenus*) is a long-distance Palearctic migrant, whose western European population reportedly makes a non-stop flight from England or northern France across the Mediterranean and the Sahara desert. We found, however, that a small part of this population makes a stopover in Iberia. By analysing the intensity and timing of migration of Sedge Warblers in both the pre- and post-breeding passages in a reedbed in central Spain during 1995–1999, we found a regular across-years influx of migrant Sedge Warblers settling in the study area. Mainly Dutch, British, and in lower proportions other western European populations, used the reedbed as a stopover area and showed a certain degree of migratory site fidelity. The timing of migration was in accordance to that expected according to latitude of the area and previously published data, and was roughly coincident with predictions of evolutionary theory about warbler migration. Peak spring passage occurred in the last two weeks of April, while the autumn one took place during the last two weeks of July and the first two weeks of August. The spring passage was shorter and of lower intensity than the autumn one. Juveniles passed slower, less concentrated in time and slightly later than did adults. The annual ratio of yearlings to adult birds was about 1:1, and closely matched that obtained by the „Constant Effort Sites" Project for the breeding British Sedge Warbler population. Therefore, part of the interannual variation in age ratios in the autumn passage at this site may be explained by variable across-years breeding success of British populations.

Keywords: *Acrocephalus schoenobaenus*, central Spain, migration, Sedge Warbler, stopover.

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1. Introduction

During migration a variety of bird species use different places for fattening to replace their energy for the flights. These stopovers are necessary to successfully complete migration, especially for long-distance migrants. However, stopover dynamics have not been examined in detail for many species and areas in the Paleartic–African migration route. This may be due to difficulties in sampling some dense habitats, as well as to the poor detectability of many small migrants. Determination of the role of stopovers along migratory routes is a concern in the global conservation of migratory species (Bairlein 1994, Spina 1999, Petit 2000).

In 1981, the European Union for Bird Ringing (EURING) started an all-European research programme to study the migration strategies of *Acrocephalus* species, the dynamics of postbreeding occurrence, the changes in birds' abundances across years, the directions of movements of ringed birds, and patterns in the accumulation of migratory fat (Koskimies & Saurola 1985). The Sedge Warbler (*Acrocephalus schoenobaenus*) migration has been widely studied in northern and central Europe within this project (e.g. Bibby & Green 1981, Koskimies & Saurola 1985, Literák et al. 1994, Chernetsov 1996, Basciutti et al. 1997). This long-distance trans-Sahara migrant is nowadays recognised as displaying three different migratory strategies (Ormerod et al. 1991), even if their details are not yet fully understood: (1) a direct, non-stop flight from the breeding areas to the winter quarters; (2) a flight that stops only in northern France or southern England, and (3) a migration flight with stopovers in Iberia or northern Africa before crossing the Sahara desert. Previous studies widely point to the two first strategies of migration as being more common (Bibby & Green 1981, Koskimies & Saurola 1985, Ormerod 1990; Schaub & Jenni 2000 a, b, 2001),

although evidence of Sedge Warbler stopover in the Iberian Peninsula also exists (De la Puente et al. 1997, Grandío 1998, 1999). However, little is known on the possible stopover of Sedge Warblers in the Iberian Peninsula as there have been no attempts to study the spring migration, and the strategies and migration routes are still poorly understood. Food shortages along migratory routes are one of the important reasons for the recent decline in Sedge Warbler populations (Spina & Bezzi 1990), so studies about stopover ecology and migration of Sedge Warbles are potentially valuable to their conservation prospects.

In this paper, data collected at Las Minas ringing station (Madrid) between 1995 and 1999 were analysed to examine some features of the migration of Sedge Warbler over central Spain. Our aims are: (1) to ascertain whether Sedge Warblers stopover regularly (i.e. on a yearly basis) in central Spain, (2) to determine the origin of the migrant population, and (3) to describe patterns in migration schedules according to age, by comparing their intensity, duration, and variation in temporal patterns. If a regular arrival of birds takes place, this should be detectable by ringing in every year. Homogeneous patterns of migration among years would indicate a regular use of the area, while strong changes in the arrival patterns might indicate a rather circumstantial use of the site. Finally, since adult birds may be more experienced than juveniles in selecting adequate stopover sites (Shennan 1985), the proportion of adults settled in an area should indicate its quality as a stopover site.

2. Materials and methods

The study was conducted in Las Minas Ringing Station (San Martín de la Vega, Madrid, 40.13 N 6.32 W). This area is a reedbed of *Phragmites australis* along the Jarama river, with reedmace (*Typha domingensis*), willows (*Salix alba*), poplars (*Populus alba*), and rushes (*Juncus* spp.). Birds were mist-netted once a week between April 1995 and December 1999, within a constant effort site station. A total mist-net length of 132–144 m, depending on year, placed in standard straight lines was operated for six hours from dawn.

All trapped birds were ringed and aged (juvenile vs adult) following Svensson (1992). Birds could not be aged in spring because both juvenile and older birds undergo a complete moult in the winter quarters (Ginn & Melville 1983).

The duration of migration was considered as the time period when birds were crossing constantly, from the first arrival until the last one, excluding birds separated more than 25 days of the main wave of migration.

To compare the number of captures, we used a corrected capture index allowing for differences due to mist-net length (capture index = number of captures x 100 x mist-net length^{-1}). In the annual capture index we took into account only the first capture of any individual handled more than once. We considered the peak of migration the date when the highest capture index occurred within each passage.

The origin of the Sedge Warbler populations was assessed by using the data available in the Recoveries Data Bases of the Spanish and Portuguese Ringing Schemes until February 2000, taking into account only those birds captured in the breeding areas from early-June to mid-July. Because the number of recoveries from a country depends on the number of birds ringed there, a recovery index (RI) was computed for each country, calculated as the number of recoveries in a period per one thousand birds ringed in the same period (Asensio & Carrascal 1987).

We used the age ratio (juveniles:adults) to compare the age structure of the migratory population across years with that obtained from the British Constant Effort Sites Program (CES-News 1995–1999) as an index of Sedge Warbler productivity.

To see whether the pre-breeding passage is more concentrated than the autumn one, we compared the variance of capture dates among passages and years. We used a two-way ANOVA with the absolute deviations from each individual's first capture date to the mean value for its passage as a dependent variable and year as an independent variable, resembling a Levene's test of homogeneity of variances (Sokal & Rohlf 1995). We analysed in a similar way whether adults had a more concentrated passage than juveniles.

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3. Results

A total of 261 Sedge Warblers was caught between 1995 and 1999, 27.6% of these in spring and 72.4% in autumn. Out of 186 birds that were aged in the post-breeding migration, 48.9% were adults and 51.1% were first year birds, giving a juvenile/adult ratio of about 1. Three captures were foreign recoveries, two from Great Britain and one from France. About 1% of all birds were retrapped more than a year after having been captured for the first time, 0.8% were captured in both passages of the same year, and 4% of all birds were retrapped within the same passage. Two of the birds we ringed were recovered abroad, in Belgium and Holland.

The analysis of all Iberian recoveries (n = 113) revealed that only 8.0% of the birds (n = 9) had been captured in European countries while in the breeding season, 77.8% of them being from the United Kingdom (RI = 0.011), and 22.2% from Holland (RI = 0.037). Nevertheless, birds from Scandinavia (3.8% of birds captured out of breeding season, n = 104), should also be breeders as these countries harbour the most northern European populations.

3.1 Timing of migration

The timing of migration of Sedge Warblers was rather constant across the study period, with only slight differences among years (Fig. 1). First spring arrivals occurred in the first week of April, although some birds were trapped in mid March, while the last birds were captured at the end of May. Peak numbers occurred in the last two weeks of April, when about 50% of the birds were captured. The post-breeding migration starts in the first two weeks of July, extending until the end of September or early October. Peak numbers occurred in the last two weeks of July and the first two of August, into which were concentrated 80% of the captures.

Although the spring migratory passage was particularly intense in 1995 (Fig. 1), there were no differences among years in the capture rate across two-weeks periods ($\chi^2_{24} = 35.52$, p = 0.611).

In general, the spring migration index of capture was lower than the autumn one (Mann-Whitney U test: $Z = -2.19$, $U = 2.0$, p = 0.028), and the spring passage was of a shorter duration (about one month) than the post-breeding passage (two months; $Z = -2.51$, $U = 0.5$, p = 0.012). The migratory passage was more concentrated in spring than in autumn (two-way ANOVA, passage: $F_{1, 266} = 6.83$, p = 0.009). However, it changed across years ($F_{4, 266} = 4.98$, $p < 0.001$), and the interaction between year and passage was also significant ($F_{4, 266} = 9.76$, $p < 0.001$). This was due to the fact that the passage was more concentrated in autumn than in spring in 1996 and 1998.

3.2. Autumn migration in relation to age

Adult Sedge Warblers passed slightly earlier than juveniles in all study years, despite the slight variations among years in the timing of migration (Fig. 1). Although first arrivals occurred at about the same dates (Wilcoxon test: $T = 2.0$, $Z = 0.53$, p = 0.593), adults peaked in the second half of July and resumed migration by early September, while the passage of juveniles peaked in early August and ended by late September (Wilcoxon tests: peak: $T = 0.0$, $Z = 1.83$, p = 0.068; last birds: $T = 0.0$, $Z = 1.83$, p = 0.068). The mean difference between adult and juveniles was 7–20 days depending on year. There were no differences between the frequency distributions of adult and juvenile birds within each year (Kolmogorov-Smirnov tests, in all $p > 0.5$).

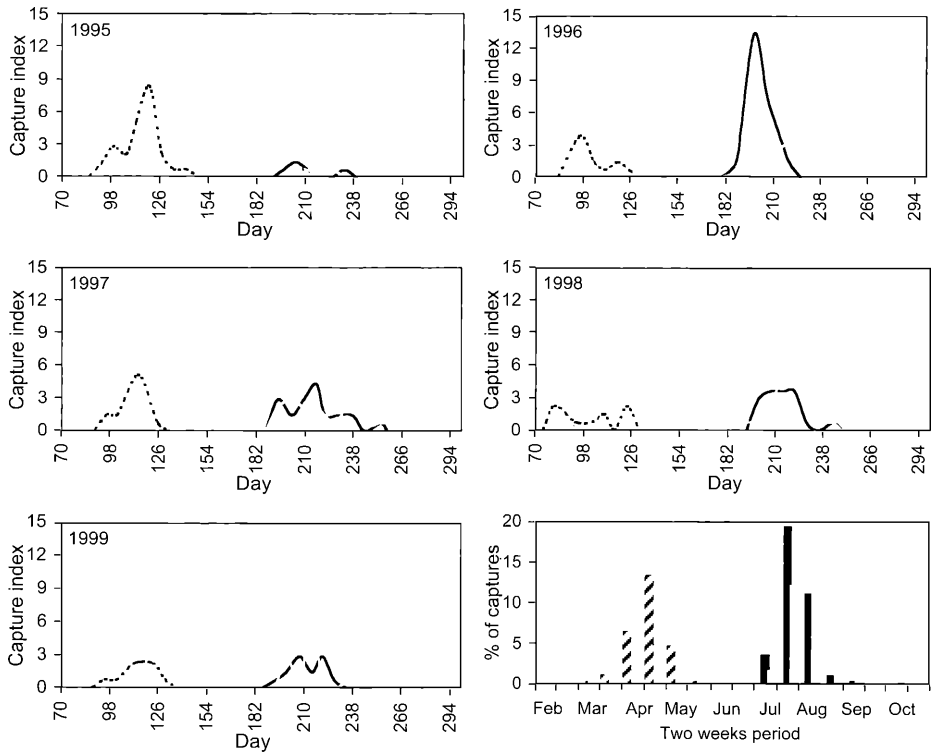

Fig. 1: Timing of migration of the Sedge Warbler in central Spain: daily capture index each year between 1995 and 1999, and percentage of total captures for each two-week period for all years pooled. Pre-breeding passage is shown in dotted line and striped bars, adult postbreeding passage in black line and black bars, and juvenile passage in grey ones.

Abb. 1: Zeitlicher Verlauf des Durchzugs von Schilfrohrsängern in Zentralspanien: täglicher „Fangindex" für jedes Jahr (1995–1999); Gesamtfänge (%) für jeden Zweiwochenabschnitt für alle Jahre zusammengefasst. Heimzug: punktierte Linien und schwarze Säulen; Wegzug (Jungvögel): graue Linien und graue Säulen.

In all years, the passage of first-year birds extended for a longer period (60 days) than adults (45 days; Wilcoxon test: $T = 0.0$, $Z = 2.02$, $p = 0.043$). Usually, only juvenile birds were recorded at the end of the post-breeding migration (Fig. 1).

On average, the extent of autumn passage changed among years (two-way ANOVA: $F_{4, 191} = 6.54$, $p < 0.0001$), and adults had a more concentrated passage than juveniles ($F_{1, 191} = 16.23$, $p < 0.0001$). However, the interaction between year and age was significant ($F_{4, 191} = 2.60$, $p = 0.038$), implying different patterns of age-related settlement depending on year (Fig. 2).

The proportion of each age class was rather constant within the autumn passage ($\chi^2_9 = 5.13$, $p = 0.823$), the age ratio being about 1:1 throughout the study period (Tab. 1). Nevertheless, there were small differences, which were significantly correlated to changes in the age ratio obtained for the Constant Effort Site Program in United Kingdom along the period 1995–1999 ($r_s = 0.9$, $p = 0.038$, $n = 5$; Fig. 3).

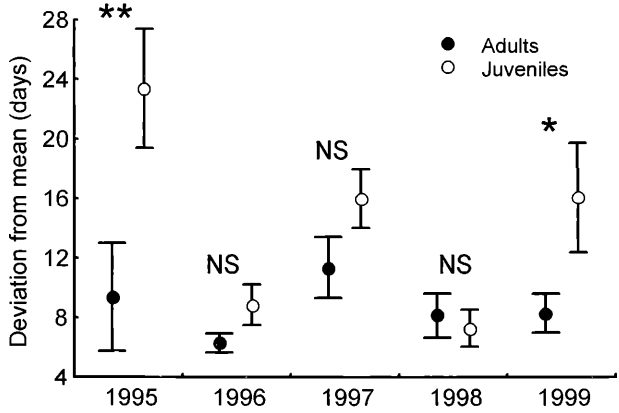

Fig. 2: Variation in the extent of the autumn passage in each study year in relation to age. The mean deviation from each bird's date of capture and the mean corresponding to each age class and year are shown (with standard errors). Labels indicate the results of Tukey tests comparing adults and juveniles within years (NS: non-significant, *: $p < 0.05$, **: $p < 0.001$).

Abb. 2: Variation im Umfang des Herbstdurchzugs von Alt- und Jungvögeln in den einzelnen Untersuchungsjahren. Dargestellt ist die mittlere Abweichung der Fangdaten für beide Altersklassen in den Untersuchungsjahren (mit Standardfehler). Vergleich Alt- und Jungvögel in einzelnen Untersuchungsjahren mittels Tukey-Test (NS: nichtsignitikant, *: $p < 0.05$, **: $p < 0.001$).

Table 1: Capture index (number of captures x 100 x mist-net length^{-1}) and age ratio of Sedge Warblers in Las Minas reedbed (central Spain) for 1995–1999.

Tab. 1: Fangindex (Anzahl Fänge x 100 x Netzlänge^{-1}) und Verhältnis Alt-/Jungvögel von Schilfrohrsängern in Las Minas-Riedflächen (Zentralspanien) für 1995–1999.

Year	Pre-breeding migration	Post-breeding migration			Total	Age ratio (juv ad)
		Adults	Juveniles	Subtotal		
1995	22.7	5.6	3.5	9.0	31.8	1.6
1996	8.0	18.6	28.6	47.3	55.3	0.7
1997	9.5	17.4	17.4	34.8	44.3	1.0
1998	7.3	20.3	15.2	35.5	42.8	1.2
1999	6.5	13.0	10.1	23.2	29.7	1.4
Total	54.0	74.9	74.9	149.8	203.8	1.0

4. Discussion

Our results show that the migration of Sedge Warblers across central Spain follows a rather consistent pattern throughout years. Taking into account that western European (British, Dutch, Belgian, etc.) populations of Sedge Warblers cross Iberia during their migration, the relative low capture rate in our study area and other places in Spain compared to other European sites (e. g. BIBBY & GREEN 1983, BASCIUTTI et al. 1997, SCHAUB & JENNI 2000a), seems to indicate that the majority of individuals undertake a non-stopping flight to Africa. So This agrees with BIBBY & GREEN (1981) although, as we have shown here, a very small part of these populations stopovers in Iberia.

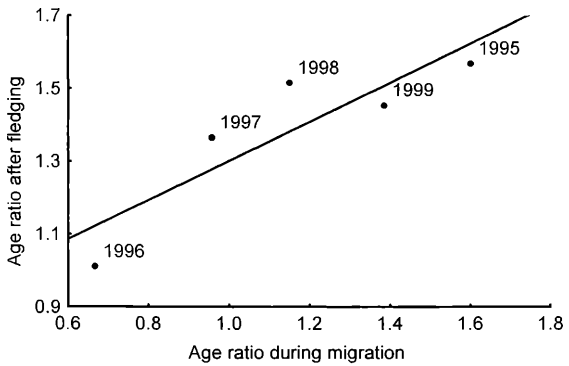

Fig. 3: Covariation between the age ratio (juveniles adults) of migrant Sedge Warblers in central Spain and that obtained in the „Constant Effort Sites" Program for the breeding British Sedge Warbler population.

Abb. 3: Kovariation zwischen dem Verhältnis Alt-/Jungvögel bei durchziehenden Schilfrohrsängern in Zentralspanien und diesbezüglichen Werten aus dem „Constant Effort Sites Program" für die britische Brutvogelpopulation.

The origin of the Spanish migrants is mainly Holland, Great Britain, and other western European countries (CANTOS 1992). The rate of foreign recoveries in Las Minas is very close to that reported for northern Spain (1.56%; GRANDÍO 1998), and higher than that in France (0.35%; JARRY 1982).

Although BIBBY (1978) suggested a lack of migratory site fidelity in Sedge Warblers, it seems that Las Minas is an habitual site of stopover in both migratory passages, as indicated by the recapture of birds in both passages of the same year. Migratory site fidelity has also been demonstrated for other passerine species in Iberia (CANTOS & TELLERÍA 1994).

As in other places (ORMEROD 1990), the migration of Sedge Warblers was of a significantly lower intensity in spring than in autumn, presumably due to the presence of first-year birds in the latter and winter mortality reducing the numbers of spring migrants (BERNIS 1966, PEACH et al. 1991). It also might be due to a faster and more concentrated migration in spring than in autumn as birds fly directly to their breeding areas (SIMMS 1985), entailing lower capture rates of migrants (BERNIS 1966, TELLERÍA 1986).

4.1 Timing of migration

The timing of Sedge Warblers migration across central Spain was similar to that reported in other studies in the Iberian Peninsula (GRANDÍO & BELZUNCE 1987, CANTOS 1992, GRANDÍO 1999), and agrees with dates reported for northern localities where birds arrive later at the breeding grounds (KOSKIMIES & SAUROLA 1985, MASON 1995, ARI 1996). In general, the passage of this species across northwest Europe appears to be consistently centered around the first two weeks of August (BIBBY & GREEN 1981, KOSKIMIES & SAUROLA 1985, ORMEROD 1990, SPINA & BEZZI 1990, LITERÁK et al. 1994), timed for an arrival to the African winter quarters in September-October (AIDLEY & WILKINSON 1987). However, birds in Finland may start migration before, in early July (KOSKIMIES & SAUROLA 1985, ARI 1996), which may be an adaptation to the longer trips and shorter favourable periods encountered at high latitudes (HAUKIOJA 1971).

The migratory timing of Sedge Warbler appears to follow a non-random and probably highly evolved pattern across Europe. This agrees with evolutionary interpretations of warbler migration (HOWLETT et al. 2000), which evidences that migrating sylviid warblers are separated ecologically by habitat use, time of passage and morphology, so that species seem to have evolved species-specific patterns of migration consistent with the idea of avoidance of interspecific competition.

4.2. Sedge Warbler timing of migration and age differences

The migration schedules of Sedge Warbler in the Iberian Peninsula differed depending on age, and adult migration occurred slightly earlier than that of juveniles. The difference between the adult and juvenile peak passages has already been noted in other studies (BIBBY et al. 1976, INSLEY & BOSWELL 1978, BIBBY & GREEN 1983, KOSKIMIES & SAUROLA 1985, RØSTAD 1986, SPINA & BEZZI 1990, CANTOS 1992, BASCIUTTI et al. 1997, GRANDÍO 1999), though peak numbers occur synchronously for both age classes in some places (GRANDÍO & BELZUNCE 1987, ORMEROD 1990, LITERÁK et al. 1994). The passage of juveniles is also more protracted than that of adults (GRANDÍO & BELZUNCE 1987, ORMEROD 1990, SPINA & BEZZI 1990, GRANDÍO 1999), and this is especially typical of low latitude areas (BIBBY & GREEN 1981, KOSKIMIES & SAUROLA 1985, SPINA & BEZZI 1990). This difference may be due to the fact that adults leave their breeding areas sooner than juveniles (INSLEY & BOSWELL 1978), because after finishing parental care, adult birds get fat and leave quickly (KOSKIMIES & SAUROLA 1985, ORMEROD 1990, CHERNETSOV 1998). Also, post-fledging movements are more pronounced than adult post-breeding movements (CRAMP 1992, CHERNETSOV 1998), and seem to be less oriented (KOSKIMIES & SAUROLA 1985, BASCIUTTI et al. 1997), which may delay their departure (INSLEY & BOSWELL 1978).

There was more variation between adults and juveniles in the timing of migration in years when there was a high juvenile:adult ratio (Tab. 1, Fig. 2), i.e. in successful breeding years. This could be related to the fact that Sedge Warblers are known to rear second broods in particularly favourable years (VAN DER HUT 1986).

The age-ratio we observed differs from those found in other studies using a constant effort mist-netting, and where first year birds were much more frequent than adults (KOSKIMIES & SAUROLA 1985, GRANDÍO & BELZUNCE 1987, SPINA & BEZZI 1990, LITERÁK et al. 1994, BASCIUTTI et al. 1997, CHERNETSOV 1998). In northern Spain, at distances lower than 500 km from our study area, the age ratio is well over 2 (GRANDÍO & BELZUNCE 1987, GRANDÍO 1999). This difference might be caused by juvenile, less experienced birds not crossing throughout the centre of the Iberian Peninsula due to more difficulties in orientation, the conditions for migration being less favourable than along the coast. However, it seems that adults and juveniles use the same route when crossing Iberia (CANTOS 1992). Alternatively, the high proportion of adults that we observed as compared to age ratios obtained in recognised stopover places in the western European migratory route could indicate a high juvenile mortality of first year birds in their trip from northern to central Spain. Further studies are needed to explain this difference in the age-ratio. Nevertheless, at least part of the variation in the age ratio among years may be explained by the breeding success in the reproduction areas, as pointed out by the correlation between the Spanish and British age ratios. This suggests that the variation in the numbers of birds crossing over central Spain is related to the breeding success of the British population, in accordance with the geographical origin of the migrant Sedge Warblers in Spain. This might therefore add a complementary perspective on breeding season success. Besides the studies developed in the breeding areas, analysing the population dynamics in the stopover and wintering areas should be a very important subject in the global conservation of migratory species.

5. Zusammenfassung

Der Schilfrohrsänger (*Acrocephalus schoenobaenus*) ist ein paläarktischer Langstreckenzieher. Vögel der westlichen Populationen (z.B. aus England oder Nordfrankreich) überqueren, wie vielfach belegt, das Mittelmeer und die Sahara im Nonstopflug. Ein kleiner Teil dieser Populationen macht jedoch sowohl auf dem Heimals auch auf dem Wegzug Zwischenstation in zentraliberischen Rastgebieten, wie die vorliegende Untersuchung zur Intensität und zum zeitlichen Verlauf des Durchzugs von Schilfrohrsängern zeigt. Während dieser Studien (von 1995-1999) in einem zentralspanischen Riedgebiet (Las Minas Ringing Station) entlang des Jamaraflust-

ses, fanden wir regelmäßig in jedem Jahr rastende Schilfrohrsänger, größtenteils niederländische und britische Vögel, aber in geringen Anteilen auch Vögel anderer westeuropäischer Populationen. Dabei zeigte sich ein gewisser Grad an Rastplatztreue. Der Zeitpunkt des Durchzugs stimmte mit Erwartungswerten bezogen auf die geographische Breite des Untersuchungsgebietes und bereits publizierter Daten überein und erfüllt auch in etwa theoretische Voraussagen zum Zugablauf bei nächtlich ziehenden Kleinvögeln. Der Durchzugsgipfel auf dem Heimzug erfolgte in den letzten beiden Aprilwochen, auf dem Wegzug in den letzten beiden Juli- und den ersten beiden Augustwochen. Der Heimzug war zudem von geringerer Intensität. Diesjährige Vögel hatten längere Rastaufenthalte, waren weniger konzentriert und erschienen etwas später im Gebiet als Nichtdiesjährige. Das jährliche Verhältnis Alt-/Jungvögel betrug etwa 1:1, wie dies auch im Rahmen des „Constant Effort Sites Project" für die britischen Populationen ermittelt wurde. Somit lassen sich jährliche Veränderungen im Verhältnis Alt-/Jungvögel beim Herbstdurchzug im untersuchten Rastgebiet z.T. mit jährlichen Änderungen im Bruterfolg britischer Populationen erklären.

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