

B. Kloubec · M. Čapek

Seasonal and diel budgets of song: a study of Savi's warbler (*Locustella luscinioides*)

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Abstract Seasonal and diel patterns of singing activity of Savi's warblers (*Locustella luscinioides*) were studied in two areas of Central Europe 300 km apart, over a period of 18 years. We assess about 4,600 records of individuals singing. Males were found to exhibit similar singing activity in both study sites. They started to sing after arrival at the beginning of April and peaked from the end of April to the beginning of May. Thereafter, their singing activity was lower but more stable for a relatively long period from mid-May to mid-July. At the end of July, males sang only sporadically and singing activity ceased at the beginning of August. At the beginning and towards the end of the song-period males sang sporadically whereas in the period of the highest singing activity they sang over the entire 24-h period. During the whole song-period, there was a significant difference in singing activity between daylight and the dark (67.2 and 32.8%, respectively). However, the period of daylight was longer. Average singing activity showed similar levels in daylight and the dark with mean numbers of 5.9 and 6.6 males per hour, respectively. Major changes in singing activity were related to the twilight periods. There were distinctive dawn and dusk choruses. In the morning, Savi's warblers exhibited similar levels of singing activity over 3 h of the dark before twilight, singing reached its highest level at twilight and 1 h after twilight. During the evening, singing activity reached its highest-level 1 h before twilight, while during twilight it

was decreasing, with a considerable decline 1 h after nightfall.

Keywords Central Europe · *Locustella luscinioides* · Singing activity

Introduction

Males of many bird species spend enormous amounts of time singing, which may amount to several hundred thousand songs per season (Møller 1991). In migratory species, song activity begins soon after arrival, followed by a steep rise to the first maximum, falls to a lower intensity, and then rises again to the second song maximum 4–6 weeks after the first (Slagsvold 1977). Male birds sing in order to acquire a mate and to defend a territory and its resources (Logan 1983; Lampe and Espmark 1987; Merilä and Sorjonen 1994; Amrhein et al. 2002) or to minimize the risk of cuckoldry by neighbouring males and to maximize the probability of their own successful extrapair copulations (Greig-Smith 1982; Møller 1991).

Diel patterns of singing vary among bird species in aspects such as the timing of peaks through the day or night and throughout the season (Staicer et al. 1996). According to Hutchinson et al. (1993), females do not much enhance their probability of pairing with a high quality male by varying responsiveness to song with the time of day; constraints on female time budgets probably have more influence on the timing of male song than does optimization of quality discrimination. Male songbirds generally have two pronounced diurnal peaks of song activity, a major dawn and a minor dusk chorus. Several hypotheses have been proposed to explain why male birds sing more intensely at dawn than later in the day. Generally, they fall into three rough classes: (1) singing more intensively at dawn could serve a function intrinsic to the singer's internal state, e.g. hormonal levels; (2) dawn singing could have a social function

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B. Kloubec
Třeboň Basin Protected Landscape Area
and Biosphere Reserve Administration,
Valy 121, 37901 Třeboň, Czech Republic
E-mail: kloubec@schkoer.cz

M. Čapek (✉)
Department of Avian Ecology, Institute of Vertebrate Biology,
Academy of Sciences of the Czech Republic, Květná 8,
60365 Brno, Czech Republic
E-mail: capek@brno.cas.cz
Tel.: +420-543-422538
Fax: +420-543-211346

(intersexual or intrasexual) that is best served at dawn; and (3) birds might sing more at dawn because of the daily timing of environmental selective pressures (Møller 1991; Staicer et al. 1996).

Our study focused on the Savi's warbler (*Locustella luscinioides*), a widespread breeder of Eurasia and northwest Africa inhabiting dense stands of vegetation in or on the edge of fresh or brackish waters. Its song is a continuous vibrant and buzzing thrill, similar to that of grasshopper warbler *L. naevia*. However, it is audibly lower in pitch and faster, less metallic in quality (Cramp 1992; Baker 1997).

Although the song of Savi's warbler is relatively well-known (Glutz von Blotzheim and Bauer 1991; Cramp 1992), little information is available on the species' singing activity and there is no comprehensive study assessing ample material. Researchers tended to study this topic only marginally (e.g. Fászl 1886; Mayaud 1930; Munn 1950; Bub 1954; Marbot 1956; Gacond 1957; Grempe 1967; Pitt 1967; Berndt and Schlenker 1974; Hasse 1974; Berndt and Busche 1979; Kostin 1983; Pikulski 1986). However, there are studies of seasonal singing activity in other birds (e.g. Slagsvold 1977; Hielt and Catchpole 1982; Greig-Smith 1982; Gottlander 1987; Lampe and Espmark 1987; Rost 1990; Puglisi et al. 1997; Gil et al. 1999; Olinkiewicz and Osiejuk 2003; Amrhein et al. 2004). Not many authors have investigated diel singing activity in birds, probably because such studies are time-consuming (but see Catchpole 1973; Sorjonen 1977; Merilä and Sorjonen 1994; Amrhein et al. 2002, 2004). Some papers are based on only a few individuals singing and/or a limited period of time (Toivari and Lindquist 1962; Kelsey 1989; Heller and Hughes 1997).

Since 1985, we have been studying seasonal and diel patterns of calling and singing activity of marsh bird species (Kloubec and Čapek 2000; Čapek and Kloubec 2002; Trnka et al. 2003). In this paper, we assess song production of the nominate Savi's warbler *Locustella luscinioides* (Savi 1824). We did not concentrate on singing activity of one or several individuals but, unlike other investigators, on all song-producing birds detectable within a particular area over a defined period of time. Singing activity was studied for 18 consecutive years. Specifically, our objectives were to: (1) determine the seasonal trend of singing activity during the song-period: what time males start and end singing, when the peak of the song period takes place and how much time it takes; (2) determine patterns of singing activity of the Savi's warbler over a 24-h period: (a) whether males sing throughout the 24-h period, (b) which time of the day they reach the peak of singing activity and whether they have pronounced dawn and dusk choruses, (c) compare the differences in singing activity between the day and night, (d) determine the influence of twilight periods on singing activity and differences in singing activity between the twilight in the morning and evening; (3) compare seasonal singing activity of the

species in two different areas; and (4) compare the patterns of singing activity in the individual years of study. The results can be used to improve surveying techniques for the Savi's warbler, for appropriate timing of field studies and interpreting the data obtained.

We use the term "twilight" for both the period from daybreak to sunrise and from sunset to nightfall. (See *The Webster's Encyclopedic Unabridged Dictionary of the English Language*, Gramercy Books, New York, 1996).

Methods

Study areas

Singing activity of Savi's warblers was studied in two areas about 300 km apart: the National Natural Reserve Parížske močiare marsh in SW Slovakia and the Třeboň and České Budějovice basins, S Bohemia, Czech Republic. The first area is located between the villages of Gbelce and Nová Vieska (47°52'N, 18°30'E) at an elevation of 120 m. The reserve is spread along the Paríž brook flowing through the marsh. It is one of the largest marshes in Slovakia, encompassing approximately 200 ha. The vegetation consists of reed stands (alliance *Phragmition communis* Koch 1926) dominated by common reed *Phragmites australis*, with, locally, patches of cattails *Typha* spp., sedges *Carex* spp., other herbaceous vegetation and various bushes and trees. Within the marsh, there are a few patches of open water surface, "lagoons", locally overgrown with marsh vegetation. The marsh is bordered by agricultural land, orchards, water-logged meadows and, here and there, by belts of bushes or trees.

In the second study area, we included 10 localities at elevations of 380–540 m; 49°00'N and 14°30'E is the approximate centre of the area. In general, the habitat included margins of fish ponds and watercourses and their immediate vicinity. They mainly consisted of reed stands dominated by common reed, while some places were overgrown with cattails, reed grass *Glyceria maxima*, sedges and others. Ruderal vegetation along ditches, belts of bushes and trees and uncultivated water-logged meadows flanked by thickets were also characteristic of the area. The study localities ranged from 0.5 to 12.0 ha in size (for other details, see Kloubec 1995).

There is a considerable difference between the study areas. The first area lies in the Pannonian Lowlands and belongs to the Pannonian section of the steppe zone. The climate is intermediate (between dry and humid). The mean annual temperature is about 9.5°C, the mean precipitation is 550–650 mm. The second area, located in the Czech Highlands, is characterized by a rather cold and humid climate, with a mean annual temperature of 7°C and mean precipitation of 600–700 mm. It belongs to the Czech section of the deciduous forest zone (Buchar 1983).

Field operations and data collected

We studied singing activity of males (see Cramp 1992, p.97, calls of adults I) irrespective of whether they were mated or unmated. We did not distinguish song-types as in the study by Pikulski (1986) and other calls (Cramp 1992) were excluded. Within the study sites, we recorded all singing males heard during survey walks along track lines. We walked at a speed of about 3 km per hour. Every singing male within earshot was recorded regardless of the distance from the line and regardless of its song duration. Each singing male was recorded only once during a single survey walk.

We performed field procedures within the two areas in the following ways. In the Parížske močiare marsh, we recorded singing Savi's warblers (and other marsh bird species) along a 3-km track line running along a dam crossing the southern and bordering south eastern part of the marsh. The elevated dam enabled us relatively easy, quiet walking without disturbing birds. We conducted 24-h censuses from February to September in 1991–2003. Within the study period, one 24-h census was undertaken in each 5-day period. Savi's warbler song was recorded in 25 censuses: 9–10, 13–15, 17–18, 22–23 and 29 April, 3, 6, 11–12, 18–19, 24–25 and 28 May, 1, 7, 13, 14–15, 22–23 and 25 June, 3, 7, 11–12, 17 and 21–22 July, 1–2, 2, 7–8 August (Fig. 1). The 24-h period was divided into survey walks 1 h in duration. The two investigators took turns in 4-h intervals and survey walks were made continuously over 24 h. In some cases they had to be interrupted (with one to several hours' break) and therefore they extended over two to three consecutive days. During a single sampling hour along a 3-km track line we recorded a maximum of 29 males singing. In all, we collected 3,812 records of individuals singing.

Within the same marsh, we carried out another survey of Savi's warbler seasonal singing activity throughout the marsh. We based our fieldwork on survey walks along a

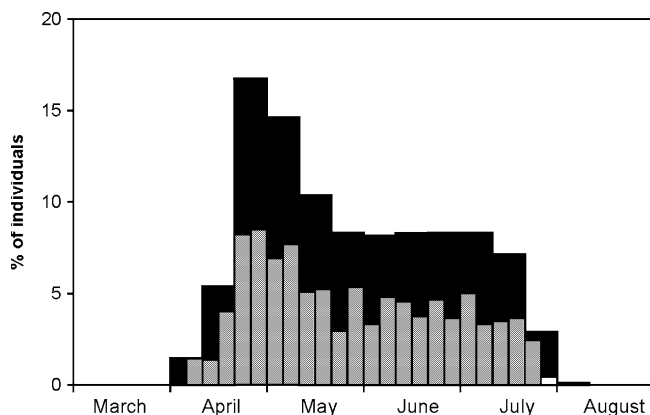


Fig. 1 Seasonal patterns of singing activity in Savi's warblers (*Locustella luscinioides*) in SW Slovakia, based on 25 24-h censuses. *Pale bars* indicate numbers of males recorded during censuses within 5-day periods and *black bars* numbers of males summed over 10-day periods ($n=3,812$)

track line, approximately 11 km in length. The walks averaged 3.5 h in duration. Surveying was only performed during the morning, usually between 0500 and 1000 hours CET (Central European Time). Song production of Savi's warblers and other marsh bird species was studied from the end of February to the beginning of September during 1985–2003 for a total of 140 sampling hours: every 5-day period was covered. We recorded Savi's warblers in 23 censuses from 10 April to 30 July (Fig. 2). During a single survey walk along a 11-km track line we recorded a maximum of 111 males singing. Savi's warbler was the second most common breeding species, with a density of 8.3–11.1 males per 10 ha giving an estimate of 166–222 males per 200 ha within the whole Parížske močiare marsh (Trnka et al. 2003). In all, we collected 676 records of individuals singing.

We also studied seasonal singing activity of Savi's warblers at 10 sites in S Bohemia along track lines with a total length of about 22 km. Censuses (2–3 h in duration) were carried out only in the morning (0500–0900 hours CET). Birds in some sites were surveyed for several consecutive years and censuses conducted over the whole season once within each 10-day period from March to August in 1987–2001. We recorded Savi's warblers in 96 censuses (survey walks) from 11 April to 19 July (Fig. 3). During a single survey walk we recorded a maximum of five males singing. In all we collected 159 records of individuals singing.

In each case, counts were made under relatively stable weather conditions. Since birds might be expected to behave unusually when faced with extremes such as rather strong wind or rain, we avoided poor weather, which could also influence the species' detectability.

Statistical analyses

Statistical analyses were carried out using *t*-test and the 95% confidence interval of the mean of a small sample (Fowler et al. 1998).

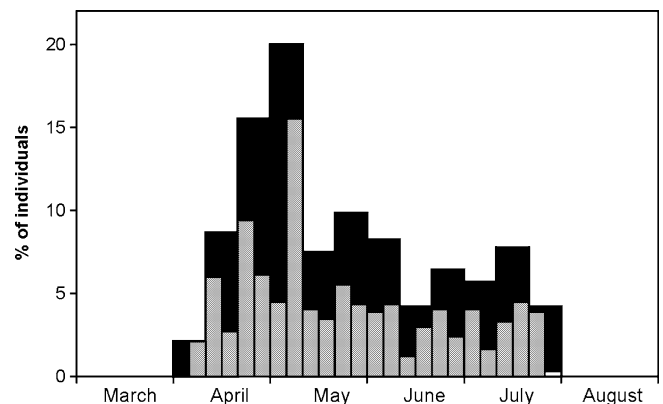


Fig. 2 Seasonal patterns of singing activity in Savi's warblers in SW Slovakia, based on 23 morning censuses. *Pale bars* indicate numbers of males recorded during censuses within 5-day periods and *black bars* numbers of males summed over 10-day periods ($n=676$)

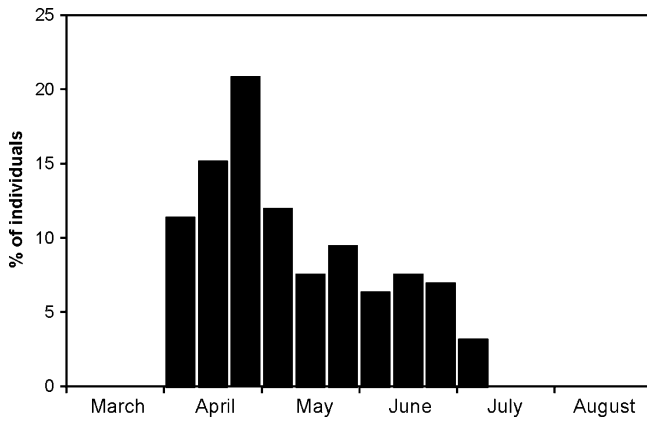


Fig. 3 Seasonal patterns of singing activity in Savi's warblers in S Bohemia, based on 96 morning censuses. Bars indicate numbers of males singing summed over 10-day periods ($n = 159$)

Results

Seasonal patterns of song

We recorded Savi's warbler song from 9 April to 8 August in SW Slovakia and 11 April to 19 July in S Bohemia (Figs. 1, 2, 3). In both the study areas, singing activity showed a similar pattern. Males sang regularly after arrival at the turn of the first 10-day period of April. Singing activity continued to increase and peaked from the end of April to the beginning of May. After that it was lower but more stable (only slightly decreasing) for a relatively long period from mid-May through mid-July. At the end of July, males sang only sporadically and, at the beginning of August (in S. Bohemia at the end of July), the singing activity ceased. If we compare the two different methods used (see Field operations and data collected), we found a slight difference in the course of seasonal singing activity recorded during 24-h and morning counts (Figs. 1, 2). In the latter method, the differences found in total numbers of males singing in particular counts were more obvious.

Diel patterns of song

At the beginning and towards the end of the song-period (9 April–8 August), we recorded the sporadic song of a few males (Table 1). There were only minor differences in the number of singing males recorded at particular hours. They sang mainly during the day, and exceptionally at night. During the period of the highest singing activity the number of males singing increased and they sang over the entire 24-h period. At the same time, the number of males singing at night continued to increase. Singing activity continued to decrease slowly from mid-May with only smaller differences in the number of males singing recorded at particular hours and more balanced ratio in numbers of males singing in

Table 1 Number of Savi's warbler males singing in the daylight and in the dark

Month	April					May					June					July					Mean							
	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2			
Numbers of males singing recorded during the 24-h censuses																												
Daylight (%)	88	62	63	66	56	68	62	65	53	70	71	70	70	69	77	75	77	79	79	65	70	75	61	65	82	100	100	71.6
Dark (%)	12	38	37	34	44	32	38	35	47	30	29	30	30	31	23	25	23	21	21	35	30	25	39	35	18	0	0	28.4
Mean numbers of males singing per 1-h periods																												
Daylight (indiv.)	3.1	2.0	6.4	13.3	11.6	9.8	10.9	7.1	6.5	4.5	8.0	5.1	6.8	7.3	5.6	7.2	5.8	5.8	6.6	6.6	4.9	5.6	4.9	3.3	0.6	0.1	0.1	5.9
Dark (indiv.)	0.8	2.1	6.5	11.8	16.1	10.0	14.3	8.1	12.4	4.1	6.9	4.6	8.0	7.4	6.4	7.2	5.2	5.2	9.5	5.5	4.8	8.3	4.7	0.3	0	0	0	6.6
Total numbers of males singing recorded during the 24-h censuses (indiv.)																												
	50	45	141	280	291	217	264	164	184	97	168	108	157	161	128	158	125	125	163	111	118	128	80	11	2	1	-	-

Based on 25 24-h censuses carried out in SW Slovakia ($n = 3,352$)
Males singing in twilight periods are not included

daylight to males singing at night. At the end of the song-period at the turn of July males did not exhibit continuous singing activity over the whole 24-h period and sang only sporadically, mostly in daylight.

Table 1 shows that there was not a similar ratio of birds singing in daylight to birds singing in the dark over the whole song-period. Averaged for the whole period, singing activity showed a slightly higher level in the dark (i.e. ca. 2100–2200 hours to 0400–0500 hours CET) with a mean number of 6.6 individuals per hour as opposed to 5.9 individuals during the hours of daylight (Table 1), but this difference is not significant (t -test, $P > 0.05$, $df=24$). Since there is a longer period of daylight than the dark in the period under study (altogether we covered 384 h during daylight as opposed to 166 h during the dark), in total, males sang more during daylight than the dark—67.2 and 32.8%, respectively.

Based on all 24-h censuses conducted, Fig. 4 summarizes the 24-h pattern of singing activity of Savi's warblers throughout the whole song-period. There were two pronounced peaks of song activity, the dawn and dusk chorus. Singing activity at both the peaks was significantly higher compared with some other parts of the day and night (for statistical analysis see Fig. 4). We recorded the highest level between 0400–0600 hours CET, and a slightly lower one between 1900 and 2100 hours CET. During the day, between the peaks, singing activity was low and more stable. The low level was also 1 h after dusk (2100–2300 hours CET) and then singing activity increased smoothly towards the morning peak.

Major changes in singing activity were related to the twilight periods (each twilight period lasts approximately 1 h), as shown in Fig. 5. During the hour at twilight in the morning, 10.8 individuals per hour sang as opposed to 7.9 individuals during the hour at twilight in the evening, but this difference is not significant (t -test, $P > 0.05$, $df=21$). In the morning, Savi's warblers exhibited similar levels of singing activity over 3 h of the

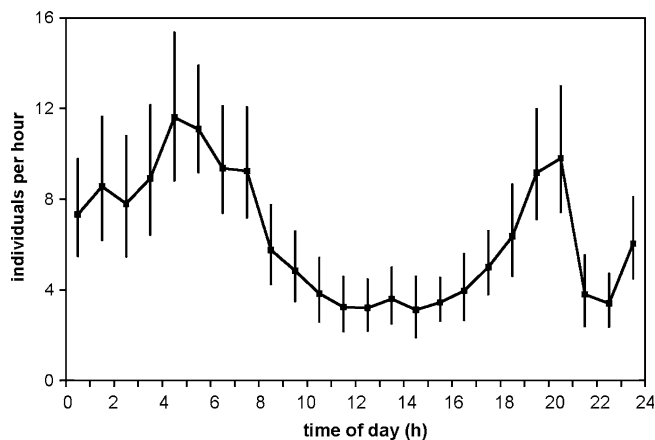


Fig. 4 Diel patterns of singing activity by Savi's warblers. Mean number of males singing per 1-h periods (mean \pm 95% confidence interval), based on 25 24-h censuses in SW Slovakia ($n=3,812$)

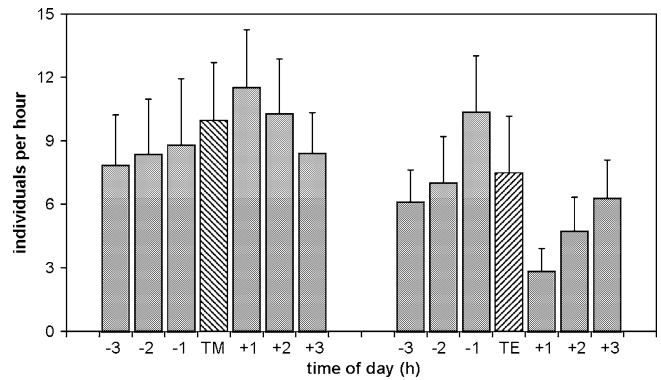


Fig. 5 Singing activity patterns of Savi's warblers during the twilight periods and during the first 3 h before and first 3 h after the twilight periods. Mean number of males singing per 1-h periods (mean \pm 95% confidence interval), based on 25 24-h censuses in SW Slovakia ($n=2,779$). Hatched bars represent times of twilight in the morning (TM) and in the evening (TE)

darkness before twilight, singing reaching its highest level at twilight and 1 h after twilight. After that, singing activity decreased to a minimum around midday. During the evening, singing activity reached its highest-level 1 h before twilight, decreased during twilight and markedly decreased 1 h after nightfall.

Discussion

Assessing the records of singing males showed a long song-period of Savi's warblers extending for 122 days within 5 months, which is the longest of all *Locustella* warblers in SW Slovakia: *L. luscinoides*, *L. naevia* and *L. fluviatilis* (Trnka et al. 2003). If the two study areas are compared, song-period in the first area located in the Pannonian Lowlands with a warmer climate and higher mean annual temperature was longer by 22 days compared with the Czech Highlands characterized by a rather cold and humid climate. However, the number of individuals singing as well as the number of censuses undertaken could play a role. Our records of first singing males in SW Slovakia correspond with those in the UK, S Moravia and Ukraine (Pitt 1967; Hudec 1983; Kostin 1983), whereas in S Bohemia, we recorded the first males singing in the second 10-day period of April as in Germany and Poland (Berndt and Busche 1979; Pikulski 1986), respectively. Song ceased by the end of July and exceptionally in early August in SW Slovakia and in the second 10-day period of July in S Bohemia; after that we did not find any individuals singing. Berndt and Schlenker (1974) and Berndt and Busche (1979) mention singing in mid-August, Grempe (1967) even up to 19 August, which might be young birds in the season of their birth (Pikulski 1986; Glutz von Blotzheim and Bauer 1991). Song-period peaked in late April and the beginning of May prior to the onset of the main season for the occurrence of eggs in the first half of May in the Czech and Slovak Republics (Hudec 1983) and other

parts of Central Europe (Cramp 1992). Pikulski (1986) showed that 32% of pairs studied commenced the second brood after successful fledging of the first. There are no data available on the percentage of second broods in the study areas. The second peak of singing activity of birds might indicate the start of the second breeding period (Slagsvold 1977). The absence of any distinctive second peak in the study areas seems to suggest that most pairs bred only once a season. It is a known fact that the singing activity of Savi's warblers decreases abruptly after pair-formation with unpaired males singing until June and July (Hasse 1974; Brendt and Bushe 1979; Bibby and Lunn 1982). The highest singing activity prior to pairing and/or egg laying has been found in many passerines (Catchpole 1973; Slagsvold 1977; Greig-Smith 1982; Gottlander 1987; Lampe and Espmark 1987; Kelsey 1989; Merilä and Sorjonen 1994; Gill et al. 1999). Unlike great reed *Acrocephalus arundinaceus* and marsh *A. palustris* warblers studied under the same conditions (Kloubec and Čapek 2000; Čapek and Kloubec 2002), Savi's warblers showed a longer period of singing activity with a peak a month earlier, and, after the decrease in mid-May, they continued to sing at a relatively stable level without distinctive fluctuations for ca. 2 months. Persistent song given almost daily appears to be typical of unpaired males (Pitt 1967; Hasse 1974).

We do not know if, or to what extent, the population size of Savi's warbler in particular years was related to its singing activity and we do not know the proportion of unpaired males or the proportion of males of the whole population which sang during censuses. Counting based on auditory detections can be underestimated as proved, e.g., by Fischer (1993) in great reed warblers. Another factor influencing the detectability of a species is the masking effect of ambient noise. Upon exposure to more sounds at the same time, the ear can perceive the louder sounds while the softer sounds are masked by the louder (Heller and Hughes 1997). According to Ryan and Brenowitz (1985), ambient noise was at relatively low levels in the early morning and was maximal at mid-day. Also, noises that include a wide range of frequencies are more effective in masking over a wide range of frequencies.

Singing activity of individual males can be related to the number of males singing in the same area (Lampe and Espmark 1987). According to Greig-Smith (1982), Female stonechats *Saxicola rubicola* with neighbours sang between breeding attempts in 71% of cases as opposed to 33% of those without neighbours. Møller (1988) found that intrusion rates by neighbouring yellowhammer (*Emberiza citrinella*) males were actually negatively related to the song activity of focal males. Colonially breeding males sang at higher rate than solitary breeding male barn swallows (*Hirundo rustica*) (Møller 1991). It is predictable that the high density of Savi's warbler (166–222 males per 200 ha) in the Parížske močiare marsh in SW Slovakia could be related to its singing activity. Moreover, we found out that some

warbler species often sing in response to sudden disturbance (see also Walpole-Bond 1933; Cramp 1992). Sometimes, a response by one male is immediately followed by a "chain reaction"—it provokes other males in the immediate vicinity to start singing (Kloubec and Čapek 2000).

In birds, as the breeding season progresses, song delivered at dawn and dusk constitutes a larger fraction of the daily total activity. Song activity patterns typically change with nesting stage (Staicer et al. 1996). Our study shows that Savi's warblers sang throughout the 24-h period with two peaks, dawn and dusk choruses, which are known to be typical of many other bird species (Kacelnik and Krebs 1983; Møller 1991; Hutchinson et al. 1993; Staicer et al. 1996). However, the 24-h pattern of singing activity tended to change with season. At the beginning and towards the end of the song-period we found only minor differences in the number of males singing at particular hours, nocturnal song was only exceptional and birds did not exhibit continuous singing activity over the whole 24-h period. In the main song-period, the highest peak of singing activity was in the morning and slightly lower in the evening with low and more stable level of singing activity between the peaks.

In total, males sang more during daylight than during the dark and in the first half of the day than the second. The Polish study (Pikulski 1986) showed most intensive song at night. However, it is based on only two 24-h samples (29–30 April and 12–13 May) and on a different method of assessing daily variation of the singing intensity (minutes per hour). In Germany, Marbot (1956) recorded the longest song shortly after midnight (26 June). In Denmark, Preuss (1967) noted the longest song bouts in the middle of the night and much shorter ones during late afternoon and earlier in day. Nocturnal song was also reported by Bub (1954) and Munn (1950). In contrast, no nocturnal song was noted in Switzerland (Gacond 1957). Other authors reported most singing in the morning and evening which corresponds with our findings (Mayaud 1930; Dementiev and Gladkov 1954). However, interpreting the above mentioned studies based on small material is questionable.

Compared with marsh and great reed warblers (Kloubec and Čapek 2000; Čapek and Kloubec 2002), Savi's warbler appears to sing more at night, but it is not a night singer only. One thing they have in common, is that its singing activity shows two peaks during the day, both the peaks being similar, whereas marsh warbler sings most in the morning and great reed warbler in the evening. Major changes in singing activity of all three species were connected with twilight periods. In great reed warblers, the singing activity increased considerably 2–3 h after twilight, in marsh and Savi's warblers it was already at a high level at twilight. In the evening, all the three species showed a rapid decrease in singing activity after twilight. Within the 24-h period, both marsh and great reed warblers reached the lowest levels of singing activity over the 2 h and 3 h before midnight, respectively, while Savi's warblers were at their lowest singing

activity at and after midday as well as between 2100–2300 hours CET.

We can speculate about the reasons for the highest Savi's warbler singing activity related to the twilight periods. Changes of light intensity around sunrise and sunset appear to be the most important proximate stimuli controlling the onset and cessation of the diurnal rhythm, although less significant changes in temperature and humidity also occur at this time (Catchpole 1973). Song concentrated at certain times, particularly at twilight, is characteristic of many birds (Møller 1991). Singing at dawn, as in the daytime, might function intrasexually, or intersexually, or both (Staicer et al. 1996). Catchpole (1973) found groups of paired sedge warbler *Acrocephalus schoenobaenus* males performing dawn and dusk choruses of "social song" even after pairing. According to Merilä and Sorjonen (1994) the diurnal pattern of song production in bluethroat *Luscinia svecica* peaked in the early morning (0300–0900 hours), with a less clear increase in song rate around 2200 hours. On the other hand, the peak of song in thrush nightingale *Luscinia luscinia* was at midnight (Sorjonen 1977). According to Hutchinson's et al. (1993) model, a male divides his time between singing and feeding. Song could act as a strategic handicap and as an honest signal of male quality. Diurnal variation in female assessment might have a profound influence on male daily routines, but dawn is rarely the best time for assessment of quality. The authors claim that females do not much enhance their probability of pairing with a high-quality male by varying responsiveness to song with time of day; constraints on female time budgets probably have more influence on the timing of male song than does optimization of quality discrimination. But females do greatly enhance their discriminatory efficiency by remembering past song output—song is then more concentrated at certain times, particularly morning. Kacelnik and Krebs (1983) interpreted the dawn chorus of the great tit *Parus major* in terms of climatic and other physical conditions in the early morning, which are unfavourable for foraging but favourable for acoustic communication and overnight accumulation of territories that favours early morning invasion by potential settlers. The combination of both factors favors early morning territorial defence, including song. Birds are more responsive to intruders when food availability is low. The high proportion of nocturnal song in Savi's warbler is worthy of notice. Since we know neither the species' breeding cycle in the study areas nor the proportion of bachelors we can only suggest the reasons for nocturnal song. Its prime function might be sexual attraction of a female in unpaired males or territorial defence in paired males. These predictions could be supported by the study of Pikulski (1986), who found higher singing activity at night in unpaired males, singing activity of paired males reached its highest level at night as well. However, no comprehensive study of Savi's warbler based on ample material exists. Intensive, mostly nocturnal song is known in related lanceolated *Locustella lanceolata*, grasshopper *L.*

naevia and river warblers *L. fluviatilis* (Cramp 1992; M. Čapek and B. Kloubec, unpublished data). Amrhein et al. (2002, 2004) found that nocturnal song in nightingales *Luscinia megarhynchos* was exhibited before pairing and during egg-laying and incubation period. Bachelors sang nocturnal song throughout the season. According to Thomas's (2002) study on the same species, singing at night is associated with increased overnight consumption of body reserves, which represents a significant metabolic cost. Nocturnal song might therefore be an honest signal of male quality. By contrast, measurements of the metabolic costs of singing in other passerines studied did not indicate significant energetic expenditure (Oberweger and Goller 2001; Ward et al. 2004). However, singing at night or at dawn instead of roosting would cause a greater increase in metabolism (Ward et al. 2003). At night, temperature gradients are much more favorable for sound transmission. In the absence of strong winds, there should also be little turbulence to scatter sound (Wiley and Richards 1982).

We can make the following recommendations for surveying Savi's warbler in C Europe. If a survey aims to record the maximum number of singing males within a certain area, the period from the end of April to the beginning of May appears to be the best time. Counts should be undertaken at twilight in the morning and 2 h after. In addition Savi's warbler should be searched for 1 h before and at twilight in the evening.

Zusammenfassung

Saisonale und tageszeitliche Gesangsbudgets. Eine Studie am Rohrschwirl (*Locustella luscinioides*)

Saisonale und tageszeitliche Gesangsaktivität von Rohrschwirlen wurden über einen Zeitraum von 18 Jahren in zwei 300 km auseinander liegenden Gebieten in Zentraleuropa untersucht. Wir betrachteten rund 4600 Aufzeichnungen über singende Individuen. Die Männchen zeigten eine ähnliche Gesangsaktivität in beiden Studiengebieten. Sie begannen nach ihrer Ankunft Anfang April zu singen und hatten einen Höhepunkt zwischen Ende April und Anfang Mai. Danach war ihre Gesangsaktivität geringer, aber stabiler für eine relativ lange Zeit von Mitte Mai bis Mitte Juli. Ende Juli sangen die Männchen nur sporadisch, und die Gesangsaktivität endete Anfang August. Am Anfang und gegen Ende der Gesangsperiode sangen die Männchen nur sporadisch, wogegen sie in der Zeit der höchsten Gesangsaktivität rund um die Uhr sangen. Während der gesamten Gesangsperiode gab es einen signifikanten Unterschied in der Gesangsaktivität zwischen Tageslicht und Dunkelheit (67,2 bzw. 32,8%), wobei allerdings die Zeiten mit Tageslicht länger waren. Die durchschnittliche Gesangsaktivität bei Tageslicht und bei Dunkelheit zeigten ähnliche Niveaus mit einem Durchschnitt von 5,9 bzw. 6,6 Männchen pro Stunde. Größere Änderungen in der Gesangsaktivität hingen mit den Däm-

merungsstunden zusammen: Es gab ausgeprägte Morgen- und Abendgesänge. Am Morgen sangen die Rohrschwirln während der drei Stunden Dunkelheit vor Anbruch der Dämmerung mit einer ähnlichen hohen Gesangsaktivität, das Maximum erreichte die Gesangsaktivität mit der Morgendämmerung bis eine Stunde danach. Am Abend erreichte die Gesangsaktivität ihr Maximum eine Stunde vor Einbruch der Dämmerung, nahm während der Dämmerung ab und sank eine Stunde nach der Abenddämmerung erheblich.

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References

- Amrhein V, Korner P, Naguib M (2002) Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Anim Behav* 64:939–944
- Amrhein V, Kunc, HP, Naguib M (2004) Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk* 121:110–117
- Baker K (1997) Warblers of Europe, Asia and North Africa. Christopher Helm, London
- Berndt RK, Busche G (1979) Ornithologischer Jahresbericht für Schleswig-Holstein 1977. *Corax* 7:127–173
- Berndt RK, Schlenker R (1974) Zum Vorkommen des Rohrschwirls (*Locustella luscinioides*) in Schleswig-Holstein und Hamburg. *Vogelwelt* 95:95–102
- Bibby CJ, Lunn J (1982) Conservation of reed beds and their avifauna in England and Wales. *Biol Conserv* 23:167–186
- Bub H (1954) Neue Beobachtungen des Rohrschwirls (*Locustella luscinioides*) am Nordwestdeutschland. *Orn Mitt* 6:219
- Buchar J (1983) Zoogeography (in Czech). SPN, Prague
- Čapek M Jr, Kloubec B (2002) Seasonal and diel patterns of song output by great reed warblers *Acrocephalus arundinaceus*. *Biologia* 57:267–276
- Catchpole CK (1973) The functions of advertising song in the sedge warbler (*Acrocephalus schoenobaenus*) and the reed warbler (*A. scirpaceus*). *Behaviour* 46:300–320
- Cramp S (ed) (1992) The birds of the western palearctic, vol 6. Oxford University Press, Oxford New York
- Dementiev GP, Gladkov NA (eds) (1954) The birds of the USSR, vol 6. Sovetskaya Nauka, Moscow (in Russian)
- Fászl S (1886) Beiträge zur Kenntnis der Schwirrsänger. I. *Locustella luscinioides* (der Nachtigallenrohrsänger) am Neusiedlersee. *Mitt orn Ver Wien (Schwalbe)* 10:303–304
- Fischer S (1993) Brut- und Gesangsphänologie des Drosselrohrsängers (*Acrocephalus arundinaceus*): Hinweise zur besseren Erfassung der Art. *Berlin Ornithol Ber* 3:9–20
- Fowler J, Cohen L, Jarvis P (1998) Practical statistics for field biology, 2nd edn. Wiley, Chichester
- Gacond R (1957) La Locustelle luscinioides *Locustella luscinioides* (Savi) a niché en Suisse. *Nos Oiseaux* 24:6–14
- Gil D, Graves J, Slater PJB (1999) Seasonal patterns of singing in the willow warbler: evidence against the fertility announcement hypothesis. *Anim Behav* 58:995–1000
- Glutz von Blotzheim UN, Bauer KM (1991) Handbuch der Vögel Mitteleuropas. Band 12/I (3.Teil). AULA Verlag, Wiesbaden
- Gottlander K (1987) Variation in the song rate of the male pied flycatcher *Ficedula hypoleuca*: causes and consequences. *Anim Behav* 35:1037–1043
- Greig-Smith PW (1982) Seasonal patterns of song production by male stonechats, *Saxicola torquata*, in summer and winter. *Ornis Scand* 13:225–231
- Grempe G (1967) Das Vorkommen des Rohrschwirls (*Locustella luscinioides*) in Mecklenburg. *Orn RdBr Mecklenburg* 5:27–36
- Hasse H (1974) Unterschiede im Gesangsverhalten lediger und verpaarter Männchen des Rohrschwirls. *Falke* 21:410–411
- Heller S, Hughes K (1997) Song activity of Henslow's sparrow and grasshopper sparrow over a 24-hour period. *Ind Audub Q* 75:61–67
- Hiatt JC, Catchpole CK (1982) Song repertoires and seasonal song in the yellowhammer *Emberiza citrinella*. *Anim Behav* 30:568–574
- Hudec K (ed) (1983) Fauna of the CSR. Birds 3/1. Academia, Prague (in Czech with a German summary)
- Hutchinson JMC, McNamara JM, Cuthill IC (1993) Song, sexual selection, starvation and strategic handicaps. *Anim Behav* 45:1153–1177
- Kacelnik A, Krebs JR (1983) The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour* 83:287–309
- Kelsey MG (1989) A comparison of the song and territorial behaviour of a long-distance migrant, the marsh warbler *Acrocephalus palustris*, in summer and winter. *Ibis* 131:403–414
- Kloubec B (1995) Bird species composition of reed stands in southern Bohemia (in Czech with an English summary). *Sylvia* 31:38–52
- Kloubec B, Čapek M Jr (2000) Diurnal, nocturnal and seasonal patterns of singing activity in marsh warblers. *Biologia* 55:185–193
- Kostin YUV (1983) Birds of the Crimea (in Russian). Nauka, Moscow
- Lampe HM, Espmark YO (1987) Singing activity and song pattern of the redwing *Turdus iliacus* during the breeding season. *Ornis Scand* 21:37–45
- Logan CA (1983) Reproductively dependent song cyclicality in mated male mockingbirds (*Mimus polyglottos*). *Auk* 100:404–413
- Marbot T (1956) Beobachtung des Rohrschwirls im Seeland. *Orn Beob* 53:201–202
- Mayaud PN (1930) La Locustelle luscinioides *Locustella luscinioides* (Savi) dans l'ouest et le centre de la France. *Alauda* 2:318–327
- Merilä J, Sorjonen J (1994) Seasonal and diurnal patterns of singing and song-flight activity in bluethroats (*Luscinia svecica*). *Auk* 111:556–562
- Møller AP (1988) Spatial and temporal distribution of song in the yellowhammer *Emberiza citrinella*. *Ethology* 78:321–331
- Møller AP (1991) Why mated songbirds sing so much—mate guarding and male announcement of mate fertility status. *Am Nat* 138:994–1013
- Munn PW (1950) Savi's warbler. *Ool Rec* 24:21–22
- Oberweger K, Goller F (2001) The metabolic cost of birdsong production. *J Exp Biol* 204:3379–3388
- Olinkiewicz A, Osiejuk TS (2003) Effect of time of season and neighbours on singing activity in the corn bunting *Miliaria calandra*. *Acta Ornithol* 38:117–122
- Pikulski A (1986) Breeding biology and ecology of Savi's warbler (*Locustella luscinioides*) at Milicz fish-ponds (in Polish with an English summary). *Ptaki Slaska* 4:2–39
- Pitt RG (1967) Savi's warblers breeding in Kent. *Brit Birds* 60:349–355
- Preuss NO (1967) Savisanger *Locustella luscinioides* (Savi) i Danmark 1964 og 1965 (in Danish with an English summary). *Dansk orn Foren Tidsskr* 61:164–167
- Puglisi L, Cima O, Baldaccini E (1997) A study of the seasonal booming activity of the bittern *Botaurus stellaris*: what is the biological significance of the booms? *Ibis* 139:638–645

- Rost R (1990) Hormones and behaviour: a joint examination of studies on seasonal changes in song production and plasma testosterone levels in the great tit *Parus major*. *J Orn* 131:403–411
- Ryan MJ, Brenowitz EA (1985) The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am Nat* 126:87–100
- Slagsvold T (1977) Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. *Ornis Scand* 8:197–222
- Sorjonen J (1977) Seasonal and diel patterns in the song of the thrush nightingale *Luscinia luscinia* in SE Finland. *Ornis Fenn* 54:101–107
- Staicer CA, Spector DA, Horn AG (1996) The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, pp 426–453
- Thomas RJ (2002) The costs of singing in nightingales. *Anim Behav* 63:959–966
- Toivari L, Lindquist O (1962) Daily singing rhythmicity of the marsh warbler (*Acrocephalus palustris*) and Blyth's reed warbler (*Acrocephalus dumetorum*). *Ornis Fenn* 39:151–154
- Trnka A, Čapek M Jr, Kloubec B (2003) Birds of the National Nature Reserve Parížske močiare Marsh (SW Slovakia) (in Slovak with an English summary). Veda, Bratislava
- Walpole-Bond J (1933) The marsh-warbler as a Sussex species. *Brit Birds* 27:58–65
- Ward S, Speakman JR, Slater PJB (2003) The energy cost of song in the canary, *Serinus canaria*. *Anim Behav* 66:893–902
- Ward S, Lampe HM, Slater PJB (2004) Singing is not energetically demanding for pied flycatchers, *Ficedula hypoleuca*. *Behav Ecol* 15:477–484
- Wiley RH, Richards DG (1982) Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Kroodsma DE, Miller EH (eds) *Acoustic communication in birds*. vol 1. Academic Press, New York London, pp 131–181