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Settlement, breeding success and song repertoires of monogamous and polygynous Sedge Warblers *(Acrocephalus schoenobaenus)*

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Abstract: Bell, B.D., Borowiec, M., McConkey, K.R. & E. Ranoszek (1997): Settlement, breeding success and song repertoires of monogamous and polygynous Sedge Warblers *(Acrocephalus schoenobaenus).* Vogelwarte 39: 87–94.

Arrival patterns, pairing dates, breeding success and song repertoires of monogamous and polygynous male Sedge Warblers *(Acrocephalus schoenobaenus)* were compared near Wroclaw, SW Poland. Polygynous males were generally amongst the first to arrive and the first to attain a mate. Both breeding success (no. young fledged) and song repertoire diversity (no. different syllable types) were greater in polygynous compared with monogamous males. The implications of these observations are discussed.

Key words: Sedge Warbler *(Acrocephalus schoenobaenus),* mating system, breeding success, song, Passeres.

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Introduction

European warblers of the genus *Acrocephalus* manifest a variety of mating systems and song characteristics (Catchpole 1980, Dyrcz 1988, Dyrcz et al. 1994, Leisler 1985, Leisler & Catchpole 1992). In one of them, the Sedge Warbler *(Acrocephalus schoenobaenus),* polygyny (bigamy) was first reported by Brown & Davies (1949), with more recent reports by von Haartman (1969), den Held & den Held (1976), Simms (1985), Borowiec & Lontkowski (1988) and Koskimies (1991).

The role of the song repertoire of the Sedge Warbler in mate attraction and in evidently advertising male fitness has been examined by Catchpole (1973, 1980), who modelled the Sedge Warbler as a monogamous species. We now extend that work by examining the breeding and song repertoires in a Polish Sedge Warbler population in which polygyny occurs (Borowiec & Lontkowski 1988). Other aspects of breeding and mating systems will be published elsewhere (M. Borowiec in prep.).

Methods

Observations were made in part of a 12 km² area of artificial water reservoirs near Wroclaw, SE Poland. The detailed investigations were conducted in tall rank herbaceous vegetation and emergent water vegetation surrounding a system of narrow drinking water reservoirs in a 15 ha study area (Fig. 1). Although the field study started in 1984 (Borowiec & Lontkowski 1988), this paper focuses on the period 1987–1995 when over 20 pairs were under observation. In 1990, only limited observations were possible.

Birds were censused and mapped daily during the arrival and settlement period from mid April through to late June, less frequently thereafter. On arrival, male Sedge Warblers immediately occupied territories and in the following days they were mistnetted and marked individually with one numbered metal ring and three colour plastic rings. Brief playback of tape recorded songs helped to establish territory boundaries. Females were caught and ringed either during incubation or, more often, when feeding nestlings.

The breeding status of all Sedge Warblers was determined, both with respect to the pair bond (e.g. unpaired, monogamous, polygynous) and nesting success. Nests were located by careful observation of adult birds. Evidence for polygyny was obtained by regular observation of colour–ringed birds. Male status was defined as follows: monogamous males have only one female mate with one breeding attempt in the season, polygynous males have overlapping pair bonds with two different females.

The songs of Sedge Warblers were recorded at Wroclaw in 1988 using a Grundig MK125 analogue tape recorder and a dynamic microphone coupled to a parabolic reflector. Initial sound analysis and coding of syllable types was carried out using Engineering Design's 486 PC bioacoustic workstation using the RTS (Real Time

Spectrogram) program. Selected song sequences were further investigated and prepared for publication on a Power Macintosh 8100AV computer using Cornell University's Canary 1.2 and Deneba Systems' Canvas 3.0.2 software.

The length of each bird's song repertoire was measured and the total number of discrete songs and elements (syllables) within each repertoire determined using laser printed output of RTS spectrograms. Standard terminology for phrases, syllables and elements in each song was used (e.g. as given by SORJONEN 1983 and CATCHPOLE & SLATER 1995). Following the method of CATCHPOLE (1976, 1979), different elements of the song repertoire were identified, each type of syllable being given a different number code. From such data, song repertoire parameters were calculated for each male (number of discrete songs, number of syllable types, number syllables/second of tape, number syllables/second of song, number discrete songs/minute). Since lengths of taped song samples varied between males (1.1–3.7 min), the first 90 s of the taped repertoire of each bird's song was taken for analysis. Statistical comparison between repertoires of monogamous and polygynous birds was then undertaken using StatSoft's Statistica 4.1 software. Because one monogamous male (No. 10) was recorded for only 64 s, it was omitted from the statistical analysis.

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Results

Breeding

Locally the average density of Sedge Warblers was 2 pairs/ha (BOROWIEC & LONTKOWSKI 1988), with an overall population in the area (12 km²) of about 250–300 pairs (M. BOROWIEC, unpubl.). The main arrival and settlement period of the Sedge Warbler extended from 15 April to 24 May, although there was annual variation over 1987–95 (M. BOROWIEC, in prep.).

The territories of all polygynous males were situated in a marshland with a mosaic of stands of *Carex* sp., *Solidago* sp., *Tanacetum vulgare,* Gramineae, *Salix* sp. and small *Populus* spp. trees. Twenty two cases of polygyny were recorded over 1987–95, amounting to almost 9% of resident paired males overall, although annually the rate varied from 0 to 13 % (Table 1). Polygynous males were generally amongst the first to arrive and the first to attain a mate; only in 1992 was no polygyny recorded (Table 1).

Table 1: Arrival an pairing dates of monogamous and polygynous males in Wroclaw study area 1987–957. – Ankunfts- und Paarungsdaten monogamer und polygamer ♂ im Wroclaw Forschungsgebiet in den Jahren 1987–95.

Year	No. paired monogamous males	No. polygynous males	Mean arrival date monogamous males	Mean arrival date polygynous males	Mean pairing date monogamous males	Mean pairing date polygynous males
1987	24	2	4 May	28 April	20 May	12 May
1988	31	3	1 May	20 April	12 May	3 May
1989	29	3	24 April	19 April	5 May	30 April
1991	33	4	1 May	27 April	17 May	12 May
1992	29	0	4 May	–	7 May	–
1993	32	3	28 April	26 April	8 May	30 April
1994	26	4	24 April	20 April	4 May	4 May
1995	23	3	25 April	23 April	15 May	3 May
1987–95	224	22 (8.9%)	29 April	23 April	11 May	5 May
1987–95[1]	195	22 (10.1%)	28 April	23 April	12 May	5 May

[1] excluding 1992 when no polygyny recorded

Table 2: Comparison of fledging success in monogamous and polygynous Sedge Warblers in Wroclaw study area 1987–95. – Vergleich des Ausfliege-Erfolgs von monogamen und polygamen Schilfrohrsängern im Wroclaw Forschungsgebiet in den Jahren 1987–95.

Adult status (n)	No. young fledged mean (SD)	No. fledged as % of eggs laid
Males		
Monogamous (130)	3.3 (2.8)[1]	54[2]
Polygynous (22)	7.7 (9.8)[1]	71[2]
Females		
Monogamous (130)	3.3 (2.8)[3]	54[3]
Primary polygynous (22)	3.9 (2.2)[3]	68[3]
Secondary polygynous (22)	4.2 (1.9)[3]	75[3]

[1] significantly different (t=6.260, p<0.001);
[2] significantly different (χ2=18.75, p<0.001);
[3] not significantly different (p>0.05) using Mann–Whitney U–tests on monogamous vs. primary polygnous; monogamous vs. secondary polygynous; primary polygynous vs. secondary polygynous.

Polygynous males arrived on average 4.9 days earlier than monogamous males (n=7, SD=2.8). At one extreme, in 1988 they arrived on average 11 days earlier than monogamous males, while in 1993 and 1995 they averaged only 2 days earlier (Table 1). The difference between the mean arrival dates of the two groups of males was significant (t=2.698, p<0.01). The mean pairing date of polygynous males was also significantly earlier than monogamous males (by 6.7 days; t=2.14, p<0.05).

The breeding success (no. young fledged) of polygynous males was greater than that of monogamous males (Table 2). The breeding success of both primary and secondary females of polygynous males also tended to be greater than for monogamous females (Table 2), but the differences were not significant (p >0.05).

Over the period of study, 378 eggs were found in nests of polygynous birds, 1162 in nests of monogamous birds. The breeding success expressed as the percentage of eggs producing fledged young was again higher in polygynous compared with monogamous pairs (Table 2). This was due to a significantly higher failure rate from predation in 126 monogamous Sedge Warbler nests (50.9%) compared with 42 polygynous nests (16.7%; χ^2=22.3, p<0.001).

Song repertoires

In 1988 songs were tape–recorded for 12 males of an intensively studied group of 18 males, two of which were polygynous (Fig. 1).

Bioacoustic data for song repertoires of these twelve males are shown in Table 3, with cumulative frequencies in Fig. 2. Over the first 90 s of recording time, the number of songs ranged from 2 to 7, the syllable types from 12 to 33, and the syllable delivery rate from 2.02 to 4.69 syllables/s (2.40 to 5.14 syllables/s if between-song intervals are excluded: see Table 3). Polygynous males had a significantly larger mean repertoire size (no. different syllable types) than monogamous males (means 32.0 and 20.9 respectively; MANN–WHITNEY U test, Z = –2.121, p <0.05). There was no significant difference in the delivery rate measured as either songs/min or as syllables/s (Table 3), nor were there significant correlations between the number of syllables and breeding success, arrival date, or pairing date (SPEARMAN rank correlations, p>0.05).

The accumulation rate of new song types was clearly greater in the two polygynous males compared with the ten monogamous males (Fig. 2). Representative samples of the songs of the po-

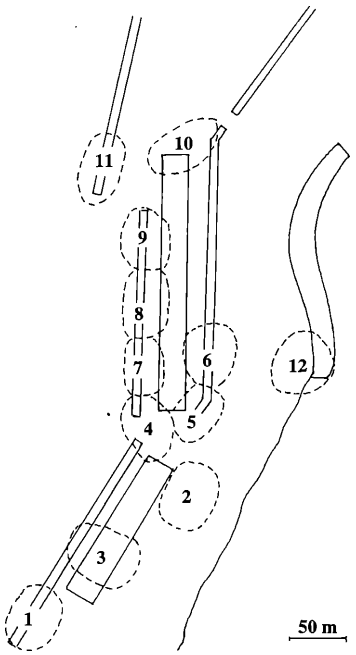

Fig. 1: Distribution of territories of tape-recorded Sedge Warblers in the Wroclaw study area in 1988. Continuous lines – water margins; interrupted lines – territory boundaries with male reference number in the middle. – Revier-Verteilung der mit Tonband aufgenommenen Schilfrohrsänger im Wroclaw-Forschungsgebiet im Jahre 1988. Durchgehende Linien – Teichufer; durchbrochene Linien – Reviergrenzen mit den männlichen Referenznummern in der Mitte.

lygynous and monogamous males illustrate the more varied repertoires of the two polygynous birds (Fig. 3). In the 6 s samples shown, polygynous males had at least nine syllable types, while monogamous males had 3–7 syllable types. The trend for greater syllable diversity in polygynous males was also evident in other years, even though the birds concerned were not tape–recorded: song repertoires were subjectively judged (by ear) to be at least amongst the most diverse of the male Sedge Warblers present (M. Borowiec, pers. obs.).

Discussion

Breeding

Emlen (1996) noted that recent data have shattered the idealistic picture of monogamous birds „working tirelessly together to feed and protect their young", stating that the „myth" of the faithful monogamous pair has been rocked by widespread findings of high rates of extra–pair copulations in many species, and species previously presumed to be monogamous are not. The Sedge Warbler is one such case. Previously regarded as essentially monogamous, we now show it to be frequently polygynous (Table 1), and molecular studies of paternity now in progress will explore the extent of extra pair matings that occur in the Wroclaw study population (M. Borowiec, unpubl.). Among European *Acrocephalus* species, Leisler & Catchpole (1992) noted that in both environment and parental care the Sedge Warbler had the most potential to develop polygyny.

Dyrcz (1988) noted that monogamy may be the original mating system in marsh–nesting European passerines, and he speculated that the inclination to partial polygyny, found in most species including the Sedge Warbler, might be of relatively recent origin and could be connected with habitat changes facilitated by humans. In contrast, in species of drier, less open habitats polygyny is less prevalent (Dyrcz 1988) – a trend also evident in North America (Verner & Wilson 1966).

The Great Reed Warbler *Acrocephalus arundinaceus* is regularly polygynous (Saitou 1976, Dyrcz 1977, Beier 1981, Ezaki 1981, Bensch et al. 1987, Catchpole 1988, Urano 1994), while the Aquatic Warbler *Acrocephalus paludicola* is promiscuous (Schulze–Hagen et al. 1993). Dyrcz et al. (1994) suggested that in four *Acrocephalus* species, including the Sedge Warbler, the mating system affects the rate of nestling growth via the degree of male emancipation. Nestling growth was fastest where both sexes feed the young – in the monogamous Reed Warbler *A. scirpaceus* and opportunistically polygynous Sedge Warbler. In the quasi–promiscuous and uniparental (female) Aquatic Warbler it was slowest, while in the facultatively polygynous Great Reed Warbler it was intermediate.

Are polygynous Sedge Warblers more successful in reproduction than monogamous birds? The available evidence indicates this to be the case (Table 2, M. Borowiec unpubl.). Analysis of

Table 3: Settlement, fledging success and song repertoire variation in monogamous and polygynous Sedge Warblers in Wroclaw study area in 1988. Polygynous males are shown in bold an male numbers relate to territories shown in Fig. 1. Song parameters are compared over the first 90 seconds of each male's repertoire. – Ansiedlung, Ausfliege-Erfolg und Gesangs-Repertoire von monogamen und polygamen Schilfrohrsängern im Wroclaw Forschungsgebiet im Jahr 1988. Daten polygamer ♂ im Fettdruck, ♂-Nummern beziehen sich auf Reviere in Abb. 1. Gesangs-Parameter werden jeweils für die ersten 90 s ♂-Repertoires verglichen.

Male ref. no.	Male arrival date	Pairing date 1st female	Pairing date 2nd female	Type of pair bond	No. young fledged	No. discrete songs	No. syllable types	No. min of song	Syllables per s overall	Syllables per s of song
1	26/4	16/5	–	monogamy	0	4	23	1.37	4.69	5.14
2	19/4	16/5	–	monogamy	4	4	18	1.27	3.93	4.69
3	29/4	9/5	–	monogamy	6	4	21	1.42	3.98	4.22
4	**21/4**	**6/5**	**16/5**	**polygyny**	**4+5**	**2**	**33**	**1.47**	**3.94**	**4.05**
5	2/5	6/5	–	monogamy	0	5	24	1.28	3.21	3.77
6	**19/4**	**7/5**	**20/5**	**polygyny**	**4+5**	**7**	**31**	**0.98**	**2.40**	**3.69**
7	2/5	4/5	–	monogamy	5	5	14	1.27	2.02	2.40
8	2/5	7/5	–	monogamy	0	4	23	0.93	2.99	4.77
9	2/5	6/5	–	monogamy	6	3	21	1.37	4.59	5.04
10*	26/4	3/5	–	monogamy	6	3	12	0.87	3.42	4.21
11	2/5	11/5	–	monogamy	0	6	22	1.32	4.23	4.81
12	2/5	8/5	–	monogamy	4	2	22	1.47	3.92	4.03

* Male no. 10 recorded for < 90 s so not included in statistical analysis (see text)

mating success in the study population at Wroclaw over many years suggests that the first–arriving males pair with an initial female very soon, then resume singing and are hence more likely to attract a second female and become polygynous, compared with other males.

While in numeric terms polygynous males produce the most fledglings, does this incur a cost in terms of fledgeling quality and survival? We found in supplementary studies (M. BOROWIEC, unpubl.) that where polygynous males raised broods with two females, the risk of the second female having lighter (=poorer) young is evidently slight: the average seventh day nestling mass did not differ significantly from that of monogamous pairs. We also found that polygynous males produced more offspring recruits compared with monogamous males: only 1.3% of 301 nestlings ringed in monogamous male nests returned to the study area, compared with almost 6% of 85 nestlings ringed in polygynous male nests (χ^2=6.04, p=0.014; M. BOROWIEC, unpubl.).

Song repertoires

When comparing the song repertoires and mating systems of six *Acrocephalus* species, CATCHPOLE (1980) argued that the songs of polygynous species had evolved primarily through intrasexual selection pressure, which produced shorter, simpler and more stereotyped sounds used mainly in male–male interactions. This situation occurred in the Great Reed Warbler and in the Aquatic Warbler. In what he regarded as four monogamous *Acrocephalus* species (Reed Warbler, Marsh Warbler A. *palustris,* Moustached Warbler *A. melanopogon* and Sedge Warbler) songs were longer, more complex and more variable, and he argued that this was due to strong intersexual selection.

CATCHPOLE (1980, 1981a,b) suggested that for the monogamous Sedge Warbler sexual selection had led to its song becoming an „acoustic peacock's tail" functionally evolved for mate attraction. Male Sedge Warblers with more complex songs were able to attract a mate before their rivals. Under controlled laboratory conditions, captive, hormone–implanted females display more to play-

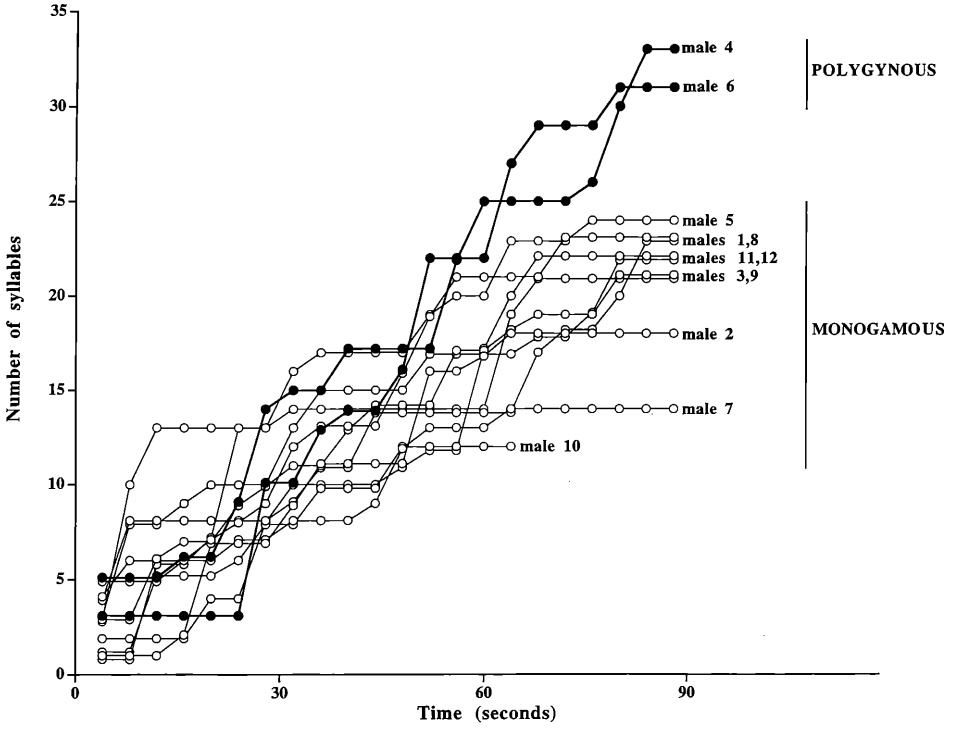

Fig. 2: Accumulation of new syllable types in the first 90 s of repertoires of monogamous and polygynous males. Male 10 was only recorded for 64 s. Male numbers are as in Fig. 1 and Table 3. – Anhäufung neuer Silbentypen in den ersten 90 Sekunden der Repertoires von monogamen und polygamen ♂. „♂ 10" wurde nur für 64 s aufgenommen. ♂ – Nummern wie in Abb. 1 und Tab. 3.

back of high repertoire song than to low repertoire song (CATCHPOLE et al. 1984), emphasising the importance of intersexual selection in the evolution of the male's elaborate song. Field studies on the Great Reed Warbler showed that in this facultative polygynous species (DYRCZ 1988) the males with larger syllable repertoires also attracted more females (CATCHPOLE 1986), and in the laboratory CATCHPOLE et al. (1986) showed that females responded more to larger repertoires.

Given these earlier observations, it is of interest to find now that polygynous male Sedge Warblers had significantly larger syllable repertoire sizes than monogamous males (Table 3, Figs. 2 & 3). This suggests that females prefer males with more complicated songs, confirming the earlier results of CATCHPOLE (1980, 1981a,b), but requiring some qualification to the broad distinctions between monogamous and polygynous species that were used to compare repertoires and mating systems within the genus *Acrocephalus*.

In reaching conclusions regarding Sedge Warbler polygyny and song repertoire size, we are of course constrained by the relatively small sample of songs analysed in this study. The results are therefore only indicative, although they do support the notion that the Sedge Warbler's complex and variable song evolved under strong sexual selection pressure, as CATCHPOLE (1980, 1981a,b) proposed. Further work on a larger sample of polygynous and monogamous males would usefully test these initial findings.

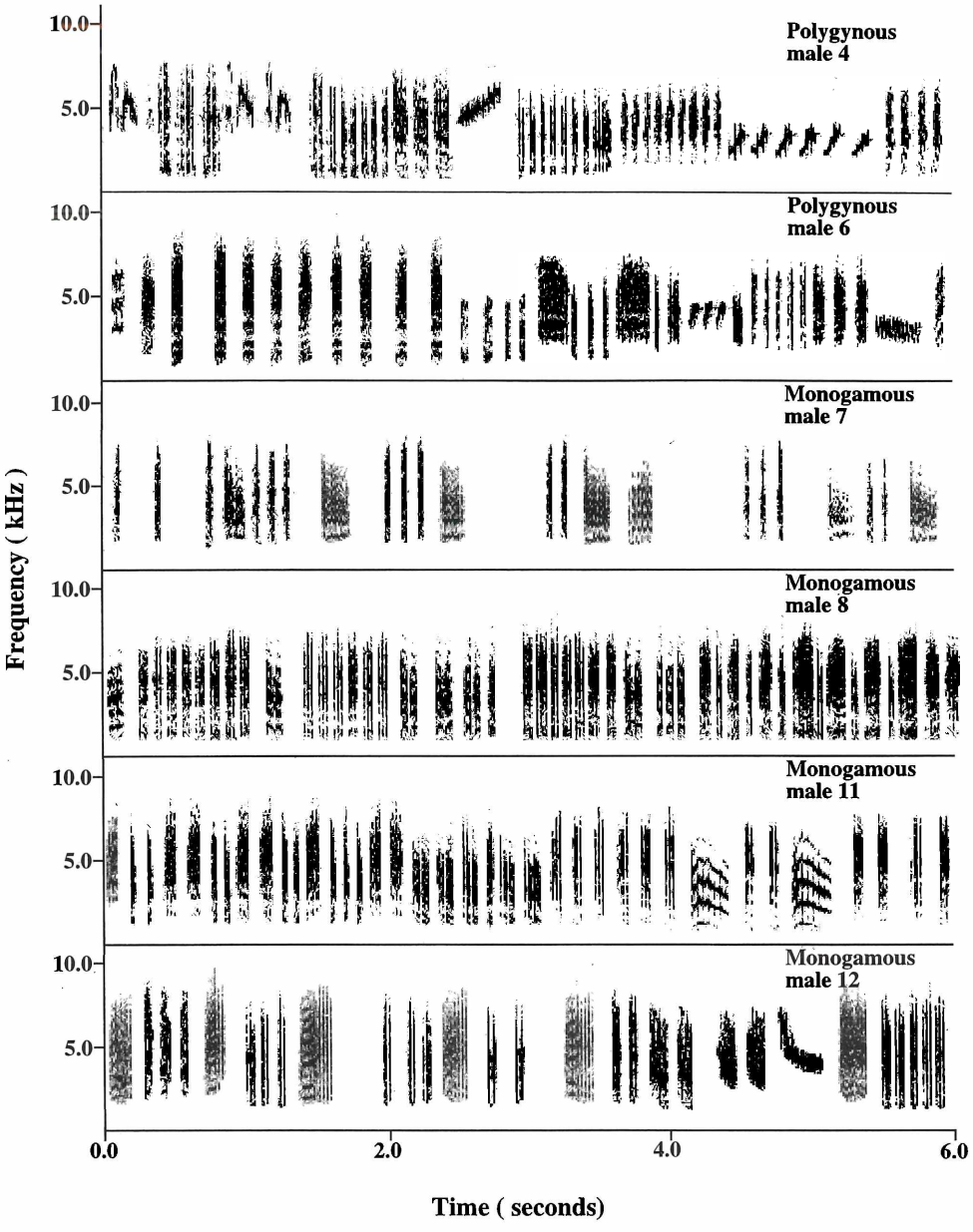

Fig. 3: Song spectrograms of a sample of six Sedge Warblers. Male numbers are as in Figs. 1 & 2 and Table 3. – Gesangs-Spektogram von sechs Schilfrohrsängern. ♂– Nummern wie in Abb. 1 & 2 und Tab. 3.

Zusammenfassung

Ansiedlung, Bruterfolg und Gesangsrepertoire monogamer und polygamer Schilfrohrsänger *(Acrocephalus schoenobaenus)*.

Ankunftsmuster, Paarbildungszeiten, Bruterfolg und Gesangsrepertoire monogamer und polygamer Schilfrohrsänger (*Acrocephalus schoenobaenus*) wurden in der Nähe von Wroclaw, Südwest Polen, verglichen. Polygame ♂ waren allgemein unter den ersten Ankömmlingen und die Ersten, die einen Partner bekamen. Bruterfolg (Anzahl flügger Nestlinge) und Gesangsvielfalt (Anzahl der verschiedenen Silbentypen) waren bei polygamen ♂, größer als bei monogamen. Schlußfolgerungen aus diesen Feststellungen werden diskutiert.

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