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Organization, variation in time, and impacting factors in the song strophe repertoire in the Great Reed Warbler (*Acrocephalus arundinaceus*)

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The song of the Great Reed Warbler (GRW) is produced by males before and during the breeding season in territory defense and mate attraction. To date, researchers studying the song of the species have mainly focused on syllable repertoire and its function. In this paper we present first data on the organization of strophes and their possible function in the GRW. We analyzed short- and long-term changes in strophe repertoire size and composition and the relationship between strophe repertoire and male age, philopatry and harem size. Syllables were organized in quite a large but still limited number of strophe types and variants, which were repeated by an individual male in the same or a relatively similar form within a season. Longitudinal analyses revealed significant effects of season and male age on strophe repertoire size. We also found a positive correlation between male harem size and strophe repertoire size. The composition of GRW strophe repertoire was stable within a season but significantly changed between years. At 3-year time intervals, GRW males exchanged more than half of their song types and almost all song variants. The level of between-year changes in song repertoire suggests that the GRW is a species adapted for learning.

1. Introduction

Bird song in many species appears to be a very complex means of communication. It has been demonstrated that, primarily, song functions in territory defence (Hyman 2002, Brumm & Dietmar 2004), mate attraction (Anderson 1994, Reid *et al.* 2004) and in some species in stimulating females for reproduction (Ballentine *et al.* 2004, Vallet *et al.* 1998).

Certain species use a single song to fulfill these aims, such as the White-browed Warbler (*Basileuterus leucoblepharus*) (Aubin *et al.* 2004). However, others produce numerous songs of amazing diversity and complexity, such as the Nightingale (*Luscinia megarhynchos*) (Kipper *et al.* 2004). In the latter case, songs commonly consist of repertoires that are more or less characteristic for an individual bird.

The origin and importance of repertoires have been intensively studied for decades, resulting in a number of hypotheses. One of the earliest assumptions was that repertoires evolved as a result of intersexual selection (Nottebohm 1972, Catchpole 1973). In this scenario, the quality of males should be positively correlated with repertoire size. Several studies support such assumptions and demonstrate that males with larger repertoires are in better condition or arrive earlier at their breeding site (Galeotti *et al.* 1997, Hasselquist *et al.* 1996, Hasselquist 1998, Hofstad *et al.* 2002, Kipper *et al.* 2006). Natural selection would in turn favour females with a preference for wide repertoires, as they would produce more or better-quality offspring.

Although this hypothesis has gained substantial support from field and experimental studies, especially showing females to prefer males with larger repertoires (Catchpole *et al.* 1986, Hasselquist *et al.* 1996, 1998, Buchanan & Catchpole 1997, Mountjoy & Lemon 1995, Searcy 1992, Eens *et al.* 1991), certain confounding factors might have been the prime targets for female preferences, such as territory quality, male age and experience, which correlate with male song-repertoire size (Forstmeier & Leisler 2004). In fact, a number of studies have not found significant connections between male repertoire and its reproductive success (for a review, see Byers & Kroodsma 2009). Thus, the connection between female preferences and the function of song repertoires may be indirect, suggesting a different origin and function of the latter.

Repertoires may also serve in territory defense and could have evolved as a result of intrasexual selection (Nowicki *et al.* 1998; but see Balsby & Dablesteen 2001). In this model, large-repertoire males are more successful in the male–male competition for high-quality territories, and reproductive difference is in turn a reflection of the variation in territory quality. There are two possible mechanisms of using songs and repertoires in male–male interactions. The first hypothesis assumes that song repertoires allow conventional signaling instead of physical encounters. If it is important in territory defense to match the songs of a neighbour, larger repertoires may allow an individual to match songs with more neighbours (for a review, see Vehrencamp 2001). Yet, song matching may not be primarily aggressive in function. According to the Acoustic Camouflage hypothesis (Craig & Jenkins 1982), birds that match the dialect elicit less aggressive response of the territory owner than strangers (Baker *et al.* 1981, Briefer *et al.* 2008). The pressure on intruders to match may be countered by a pressure on residents to make the matching of their songs more difficult. Repertoires might therefore have evolved to make matching more challenging for strangers, and so prevent them from settling.

Other hypotheses suggest, for example, that repertoires evolved in the context of density assessment (Krebs 1977) or habituation avoidance (Krebs & Kroodsma 1980). Both emphasise the main function of song repertoires in intrasexual interactions.

Song repertoires differ among species. In some of them, such as the Great Tit (*Parus major*), a male sings a number of distinct strophes (Lambrechts & Dhondt 1990) which are characterized by specific sequences of syllables. The repertoire size in this case means the number of different strophes. In other species, such as the Sedge Warbler (*Acrocephalus schoenobaenus*), songs are composed of rather random sequences of syllables that are rarely repeated in the same order. In such situations repertoire size refers to the total number of syllables used by an individual (Gil & Gahr 2002, Nicholson *et al.* 2007).

Although above-cited authors often use the term “song repertoire” in both contexts, the appropriate form of the former should be “strophe repertoire” and the latter “syllable repertoire”, which distinguish between the two kinds of repertoires. The repertoire of the Great Reed Warbler (hereinafter “GRW” for brevity) has been estimated in previous studies to be similarly to that of the Sedge Warbler, i.e., as the number of different syllables used by the male, thus concerning syllable repertoire. The only remarks on strophes in the GRW come from Catchpole (1980, 1983) who concluded that “there is no attempt to repeat stereotyped song types”. Contrary to this finding, during our four-year study on the vocal behaviour of GRW we have observed a high level of repeatability of the same or similar strophes produced by individual males throughout the breeding season.

In the present paper we describe the organization of strophes and strophe repertoires in GRW and their possible function for the first time. We analyse short- and long-term changes in strophe repertoire size and composition and a relationship between strophe repertoire and male age, philopatry and harem size. We then compare our results to our recent report of GRW syllable repertoires (Węgrzyn & Leniowski 2010).

2. Material and methods

2.1. Study area and population

We conducted the study during 2002–2005, from the end of April to the beginning of August each year. The study area consisted of ten fishponds situated in Korniaktów Północny near Rzeszów, south-eastern Poland (50°07'20" N, 22°22'23" E). We mist-netted and colour-ringed all territorial males within the study area ($N = 42$ different individuals over the four years). However, due to the difficult accessibility of three territories, we recorded and analyzed only 39 males. We monitored all territories every 2–4 days during the breeding season and collected data on the identity, status and vocal behaviour of each male. In 2002 we only recorded the vocal behaviour of males, but in 2003–2005 we also estimated each male's harem size and breeding success. Since 2003 we carefully checked all territories for nests and nestlings that were, if encountered, fitted with metal rings (for details, see Węgrzyn *et al.* 2010). During 2003–2005 we ringed 191 nestlings. The pairing success of males was measured as the number of females nesting together with a given male (i.e., harem size). We were able to assign a particular male to a particular female because males actively defended the nests of their females.

In the genus *Acrocephalus* it is not possible to age individuals on the basis of plumage, because first-year and older birds look the same. To perform longitudinal analyses of changes in the size and the composition of strophe repertoire we assigned males to categories according to the number of study seasons in which the male was encountered. Males recorded for the first time were scored as 1+ and consequently 2+, 3+ and 4+ when recorded in consecutive years. This method of estimating minimum age has been used in previous studies on repertoire size in migratory warblers (Gil *et al.* 2001, Nicholson *et al.* 2007, Węgrzyn *et. al.* 2010, Węgrzyn & Leniowski 2010).

In analyses on the effect of philopatry on song repertoires, we divided the males into two groups: PHILOPATRIC (2+, 3+, 4+) and NEWCOMERS (1+). The first year of the study (2002) was excluded from this analysis as all males were observed for the first time, making it impossible to distinguish returning individuals from new ones. We ringed all territorial males during 2002–2005 and all nestlings found during 2003–2005, and therefore the probability that a male without a ring (i.e., recorded for the first time) was new to the study area was high.

2.2. Song recording

We analyzed sizes and detailed components of the strophe repertoires of 39 males recorded between 2002 and 2005. Nineteen males had been recorded twice during the same season (10 in 2004 and 9 in 2005), and we used these to evaluate changes in strophe repertoire size and composition over a short time. For longitudinal analyses, we used the recordings of 15 returning males. We recorded two males in all four seasons, five in three seasons, and eight in two seasons. We recorded all males from a distance of 2–4 m using an AKG C568 EB shot-gun microphone and a Sony MZR 50 Mini Disc player. We analyzed the resultant sonograms using Avisoft SASLab Pro 4.x software with the following parameters: 1024 FFT length, frame (%) = 25, window = Hamming, and temporal overlap = 87.5%. This gave a 244 Hz bandwidth with 46 Hz frequency and 2.67 ms time resolution (Specht 2002).

2.3. Analyses of song repertoires

To estimate the size and composition of strophe repertoire, and their consistency in individuals within and between seasons, we catalogued all observed strophes for every male on the basis of visual inspection of sonograms containing 10-min samples of continuous singing (GRW males present their full strophe repertoire within this time period; see Results). Although the visual inspection of sonograms involves subjectivity, previous studies suggest that results obtained using this method do not differ significantly from those obtained with advanced mathematical models (Nowicki &

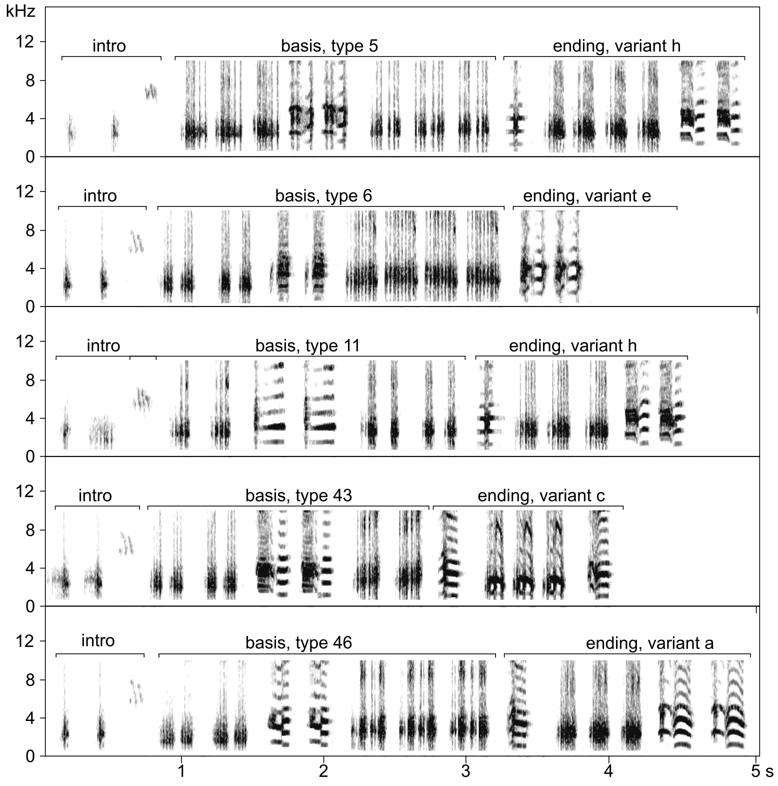

Fig. 1. Examples of different types and variants of strophes in the Great Reed Warbler: 5h, 6e, 11h, 43c and 46a. Types are distinguished based on syllable sequence in the forepart called "basis". Syllable sequence in the subsequent part of the strophe creates variants within types.

Nelson 1990, Podos *et al.* 1992, Helweg *et al.* 1990, Helweg *et al.* 1998). Also, the results of visual inspections of sonograms, performed by different persons experienced with sonograms, were convergent (Reid *et al.* 2004). In particular cases where various fragments of vocalization may be of different importance in communication, some subjectivity in strophe classification may be even more helpful than a method that objectively estimates absolute similarity (Janik 1999, Payne *et al.* 2000). Therefore visual inspection of sonograms is among the most often used methods in studies of vocal behaviour of birds (Molles & Vehrencamp 1999, Molles & Vehrencamp 2001, Wilson *et al.* 2000, Hill *et al.* 1999, Nordby *et al.* 2002).

Certain important features of strophes need to be considered while analysing and discriminating GRW songs: (1) males involved in territory encounters tend to shorten songs by deleting distal parts, (2) the repetition of a particular syllable in the same type of strophe is flexible, and (3) strophes that have the same syllable order in the forepart may differ in ending, creating variants of a particular strophe type. Therefore, we distinguished strophe types primarily according to the syllable sequence (i.e., ignoring the number of repetition of each syllable) in the forepart of a strophe following few introductory syllables. This forepart is referred to as "basis" (Fig. 1). We counted strophes with the same basis as representing the same type. We registered strophe types with numbers (1, 2, 3, etc.). We classified differences in the endings of strophes with the same basis as variants within a particular type (Fig. 2), and marked these with letters (a, b, c, etc.) preceded by a strophe-type number (Figs. 1–2). Classifying variants as different types would render the classification of shortened strophes impossible (consisting of basis only), which occurs in the GRW quite commonly. In some cases, we observed the insertion of repeated whistles in front of a basis. We marked such variants by "+". The described system of classification of GRW song enables a comparison of strophe repertoires both between years and individuals. This also simultaneously emphasizes similarities in syllable sequence within strophes of a given type (similar strophes) or variants (identical strophes).

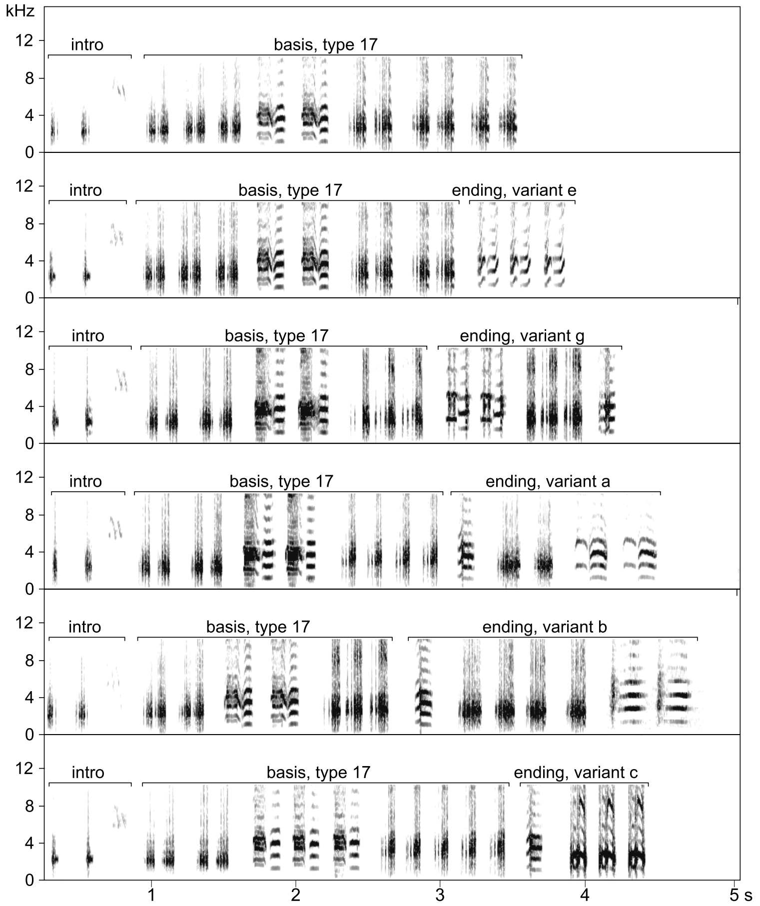

Fig. 2. Sonograms of six variants of the same strophe type (17) in the Great Reed Warbler. All strophes have the same basis but different endings. Different repetition of the same syllable does not account for different types or variants, as the males often change the number of repetitions of a given syllable before switching to another one.

To analyze changes in both strophe repertoire size and composition we used the same approach as in the analyses of GRW syllable repertoire (Węgrzyn & Leniowski 2010). We calculated changes in strophe repertoire size using the formula

$$1 - R'/R'' \tag{1}$$

where R' is the smaller repertoire size and R'' is the larger repertoire size, derived from two different recordings of a given individual. R'/R'' thus is the similarity in size of the two repertoires. To calculate changes in strophe repertoire composition we used the formula

$$1 - 2N_S / (R_1 + R_2) \tag{2}$$

where N_S is the number of the same strophes, and R_1 and R_2 are strophe repertoire sizes from two different recordings of a given male. Thus, $2Ns/ (R_1 + R_2$ provides a measure of the compositional similarity between two repertoires. In the analyses of short-term changes, we used the recordings of the same bird separated by at least six days. To analyze long-term changes, we used recordings of the same male from different seasons (longitudinal analyses). We separately calculated changes that occurred over two, three and four seasons.

2.4. Statistical analysis

Similarly to our previous study on syllable repertoire in the GRW (Węgrzyn & Leniowski 2010), we used a Linear Mixed Model with diagonal repeated covariance type to test the effects of age and season on the strophe repertoire of individuals. We included male identity as a random effect (in SPSS called "Subject") and the year of recording (1–4) to identify repeated observations. We entered stro-

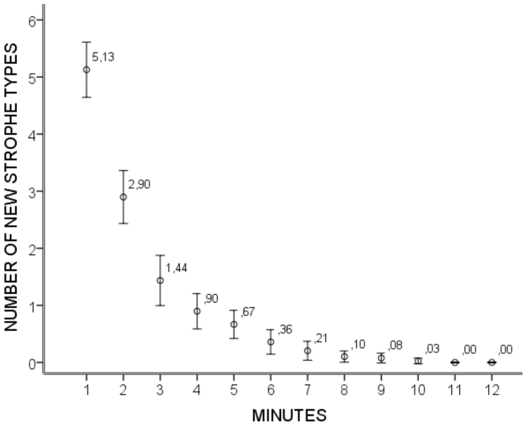

Fig. 3. Mean number of new strophe types in consecutive minutes of singing in the Great Reed Warbler (*n* = 39 males; error bars = 2SE).

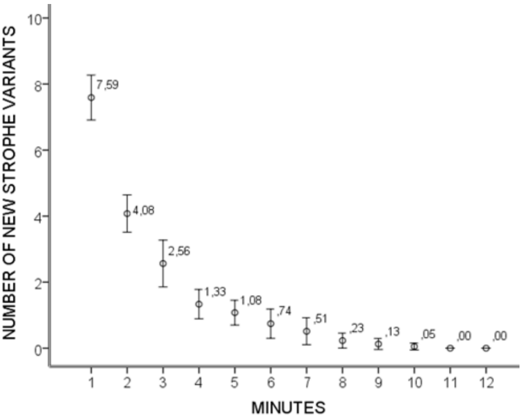

Fig. 4. Mean number of new strophe variants in consecutive minutes of singing in the Great Reed Warbler (*n* = 39 males; error bars = 2SE).

phe repertoire size (number of types and variants) as a dependent variable. Season and the minimum age of male were defined as fixed factors.

We used a Spearman rank correlation to test the relationship between strophe repertoire size and male harem size. For this purpose we ran the analysis separately for each season (21 males in 2003, 15 in 2004 and 17 in 2005) and also pooled the three seasons together to obtain a general pattern. We conducted all analyses separately for strophe types and variants. We ran all statistical analyses using SPSS and Statistica.

3. Results

3.1. General characteristics of strophe repertoires

Strophes consisted on average of 16.8 syllables (± 0.3 SE; range 4–48; *N* = 600 strophes from 20 randomly-chosen males). Males sang on average 7.0 strophes per minute (± 0.063 SE: range 3–12; *N* = 600 minutes of song of 20 randomly-chosen males). Strophe repertoire size and composition were estimated based on 10 min samples of continuous singing, as within this time GRW males presented their full strophe repertoire (Fig. 3 and 4). During 2002–2005, strophe repertoire of a male was on average 9.6 ± 2.0 SE types (range 6–15; *N* = 39 males) and 16.1 ± 5.2 SE variants (range 7–32; *N* = 39 males). Altogether we distinguished 35 types and 258 variants of strophes. Some were present only in a particular year or were specific for a given male.

In spontaneously-singing males, we also observed long songs lasting for 8–20 s with no repeatable syllable order. However, these songs made on average only about 4% of all vocalisation and were excluded from the analyses. We thus used 10-minute samples that did not contain such long songs.

3.2. Short-term changes in strophe repertoire size and composition

The sonograms revealed a high level of repeatability of same or similar strophes in the recordings of every studied male, suggesting that males possess stable strophe repertoires at least within a given season. To evaluate the stability of strophe repertoires over a short time we calculated changes in repertoire size and composition for males that had been recorded twice during a given season (*N* = 19). Within-season changes in the size and composition of repertoire, regarding strophe types and variants, are shown in Fig. 5. The low level of changes indicates high repertoire stability over a short period. The most obvious changes both in repertoire size and composition occurred in cases when long time interval between recordings coincided with a change of a territory by an unsuccessful male, or when one of the recordings was made

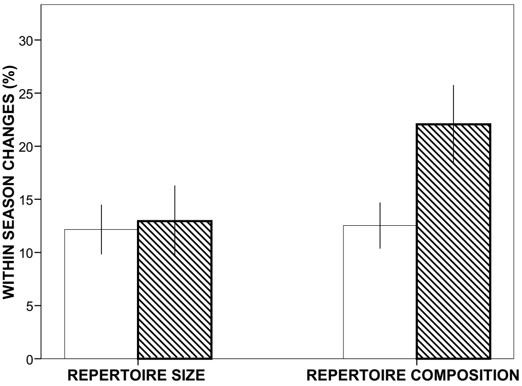

Fig. 5. Within-season changes in strophe repertoire size and composition in the Great Reed Warbler (n = 19; mean and SE). Repertoire changes were estimated separately for strophe types (hollow squares) and variants (cross-hatched squares).

in the very first or last days of the season, which resulted in a reduction in repertoire size. The rest of the cases were characterized by high repeatability in both strophe types and variants within a season.

3.2.1. Changes in strophe repertoire size

Changes in the size of repertoires of strophe types were low ($\bar{x}$ = 12%, SE = 2.34, range 0–35%, N = 19 males) and similar to changes in the size of repertoires of strophe variants ($\bar{x}$ = 13%, SE = 3.36, range 0–50%, N = 19 males; Mann–Whitney U test: Z = –0.276, P = 0.773, N = 19). Changes in the repertoire size of strophe types and variants were not directional – with the progress of breeding season strophes were dropped (types: eight cases, variants: eight cases), gained (types: six cases, variants: five cases), or the repertoire size remained unchanged (types: five cases, variants: six cases).

3.2.2. Changes in strophe repertoire composition

Changes in the composition of the repertoire of strophe types ($\bar{x}$ = 13%, SE = 2.18, range 0–33%, N = 19 males) were significantly lower than changes in the composition of repertoire of strophe variants ($\bar{x}$ = 22%, SE = 3.7, range 0–57%, N = 19 males; Mann–Whitney U test: Z = –2.018, P = 0.043, N = 19), indicating that within-season changes in repertoire composition refer more to the distal parts of strophes (strophe endings) than to the foreparts of strophes (strophe bases). However, the overall low level of change in GRW strophe repertoire composition indicates high repeatability of strophes during a season by individual males.

3.3. Between-seasons changes in strophe repertoire size and composition

Changes in the strophe repertoire size and compo-

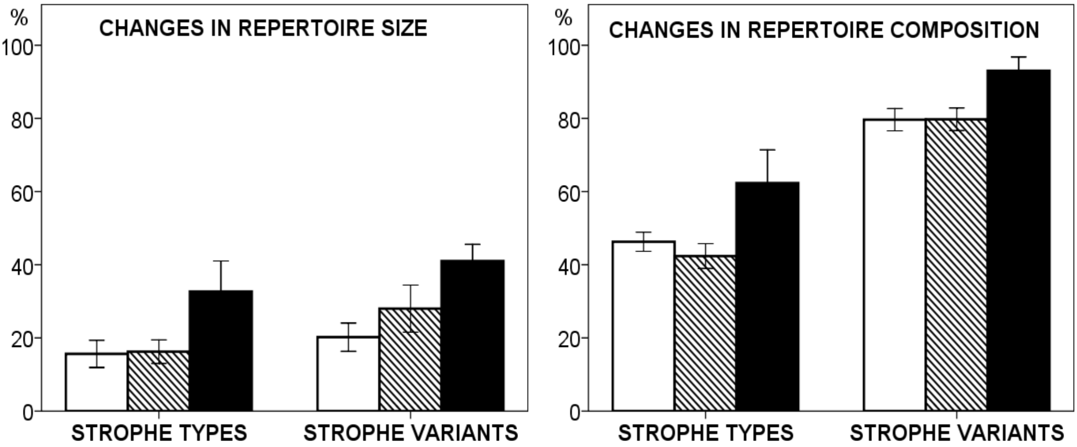

Fig. 6. Long-term changes in strophe repertoire size and composition in the Great Reed Warbler (mean and SE). Changes were counted over time intervals of 1 year (n = 14 males; open squares), 2 years (n = 8; cross-hatched) or 3 years (n = 3; filled).

Table 1. Changes in the size and composition of the strophe repertoire between seasons in the Great Reed Warbler. Time = time interval between recordings (1 = 1 year, 2 = 2 years, 3 = 3 years); *N* = the number of individuals in a longitudinal analysis.

	Change in size (%)						Change in composition (%)					
Variable	Types			Variants			Types			Variants		
Time	1	2	3	1	2	3	1	2	3	1	2	3
Mean	16	16	33	20	28	41	46	42	62	80	80	93
Min–max	0–45	0–30	18–47	0–47	0–44	32–47	22–65	33–57	50–80	60–94	64–89	87–100
SE	3.76	4.25	8.23	3.87	6.44	4.58	2.62	3.4	9.06	3.05	3.09	3.79
N	14	8	3	14	8	3	14	8	3	14	8	3

sition of a given male over multiple years were calculated on the basis of the recordings of returning males. Two males were present in all four seasons, five males in three seasons, and eight males in two seasons. Long-term changes in the size and composition of the strophe repertoire are shown in Fig. 6, and the precise values of these changes are given in Table 1.

3.3.1. Changes in strophe repertoire size

The size of strophe repertoire of individuals did not vary significantly more between than within seasons, both in terms of strophe types (Z = –0.658, $P = 0.51$, $N_1 = 19$, $N_2 = 14$) and variants (Z = –0.055, $P = 0.956$, $N_1 = 19$, $N_2 = 14$). Mean long-term change in the size of strophe-type repertoire was only slightly lower than that of strophe variants repertoire (18% vs. 25%; $Z = –1.55$, $P = 0.12$).

Regarding the effects of male age and season on changes in strophe repertoire size, we assigned all males to minimum-age categories (1+, 2+, 3+ and 4+) and to seasons in which they were recorded (2002, 2003, 2004 and 2005). The sizes of the repertoires of strophe types and variants for age categories and seasons are shown in Table 2. sentence: "LMM showed a significant effect of season on strophe-type repertoire size ($F = 4.148$, $P = 0.02$, $N = 59$) and age on strophe-variant repertoire size ($F = 7.507$, $P = 0.008$, $N = 59$). Irrespective of seasonal variation in the number of strophe types, older males sang more variants than younger ones (Table 2).

The average strophe repertoire size of philopartic males was 11.2 types (± 0.32 SE, range 7–15, $N = 15$) and 15.4 variants (SE = 0.52, $N = 15$ males; range 11–21%), while the size of the repertoire of newcomers was 9.1 types (± 0.35 SE, range 4–13, $N = 24$) and 11.3 variants (± 0.5 SE, range 4–18, $N = 24$ males). Philopatric males had significantly larger strophe repertoires than newcomers both in terms of types and variants (Fig. 7; $Z = –2.55$, $P = 0.011$ and $Z = –3.16$, $P = 0.002$, respectively; $N_1 = 15$ and $N_2 = 19$).

Table 2. Numerical parameters of repertoires of strophe types (T) and variants (V) for age categories (1+, 2+, 3+, 4+) and seasons (2002, 2003, 2004, 2005). *N* = the number of individuals in the analysis.

	Age								Season							
	1+		2+		3+		4+		2002		2003		2004		2005	
	T	V	T	V	T	V	T	V	T	V	T	V	T	V	T	V
Mean	9.11	11.26	11.08	14.75	10.75	15.38	12.67	18.00	7.88	10.50	10.35	12.50	9.33	12.20	11.06	15.41
Min–max	4–13	4–18	7–13	11–21	9–14	12–18	11–15	16–19	6–10	9–13	6–13	7–16	4–12	4–18	8–15	9–21
SE	0.35	0.50	0.43	0.77	0.59	0.94	1.20	1.00	0.44	0.42	0.44	0.60	0.58	1.00	0.45	0.82
N	35	35	14	14	8	8	3	3	9	9	15	15	21	21	17	17

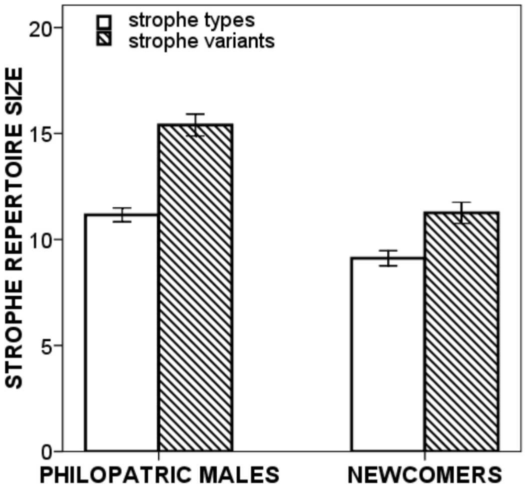

Fig. 7. Strophe repertoire size in philopatric males and newcomers in the Great Reed Warbler (mean and SE). The repertoire sizes were estimated separately for song types (hollow squares) and variants (cross-hatched squares).

3.3.2. Changes in strophe repertoire composition

Strophe repertoire composition changed significantly more between than within seasons ($\bar{x} = 46\%$ and 13% for types, and 80% and 22% for variants, respectively; $Z = -4.739$, $P < 0.001$, $N_1 = 14$, $N_2 = 19$). Over three-year intervals, males exchanged more than half of their strophe types and almost all strophe variants ($\bar{x} = 62\%$ and 93%, respectively; Fig. 5). Changes in strophe variants were significantly higher than changes in strophe types ($Z = -5.827$, $P < 0.001$, $N = 25$).

The patterns of long-term changes were different between repertoire composition and repertoire size (Fig. 6). Thus, changes in composition were significantly more frequent than changes in size for both strophe types and variants ($Z = -5.365$, $P < 0.001$ and $Z = -6.069$, $P < 0.001$, respectively; $N = 25$ for both analyses).

3.4. Relationship between strophe repertoire size and harem size

When calculated for separate seasons, correlations between repertoire size and harem size were statistically significant in every season only for strophe variants (Spearman correlation: $r = 0.38$, $P = 0.05$, $N = 21$, $r = 0.81$, $P < 0.001$, $N = 15$, $r = 0.44$, $P = 0.038$, $N = 17$ for the seasons 2003, 2004 and 2005, respectively). Strophe types correlated significantly with harem size only in 2004 ($r = 0.49$, $P = 0.034$, $N = 15$). When we used pooled data from three seasons (2003–2005), correlations between harem size and both strophe types and variants turned out to be significant ($r = 0.28$, $P = 0.03$, $N = 39$ for types and $r = 0.3$, $P = 0.023$, $N = 39$ for variants).

4. Discussion

Our analyses demonstrate for the first time that song syllables in the Great Reed Warbler are organized into a large but still limited number of strophe variants, and that there is an even less variable “basis” part (strophe type) making up the first part of each song strophe. Strophe types and variants are repeated by individual males in the same or a similar form within a season. This finding has practical significance in that, at least in the Great Reed Warbler, song analyses based on one-day recordings are representative of male vocalisations within a breeding season. The complete strophe repertoire is apparently presented within 10 minutes of continuous singing.

Consecutive recordings of banded males demonstrated a low level of changes both in the size and composition of strophe repertoires within a season. This is an important result too, as the Great Reed Warbler has commonly been regarded as having no strophe repetition. Thus, previous analyses of the repertoire in this species (Catchpole 1980, 1983, Catchpole *et al.* 1986, Leisler *et al.*1995, Hasselquist 1998, Nowicki *et al.* 2000, Forstmeier & Leisler 2004, Forstmeier *et al.* 2006, Węgrzyn & Leniowski 2010) have referred to the number of different syllables used by a male, i.e., syllable-repertoire size. Strophe repertoires, a feature of vocalization newly described in the present paper, may play an important role both in inter- and intra-sexual selection. We discuss our results and implications for further studies in the following sections.

4.1. Strophe repertoire size

Changes in the strophe repertoire size of an individual male were relatively low both within and between seasons: they rarely exceeded one or two strophes. sentences: "Season and male age had strong effects on the numbers of strophe types and variants. Despite the seasonal variation in the number of strophe types, older males sang more strophe variants than younger ones, supporting earlier studies (Hasselquist et al. 1996, Hasselquist 1998). The demonstrated effect of season on syllable-repertoire size was similar to an earlier study done in the same Great Reed Warbler population (Węgrzyn & Leniowski 2010); however, the peak years of syllable and strophe repertoires were different (2004 vs. 2005). The reasons for this seasonal variation in repertoire size remain unclear. The effect of male age on the number of strophe variants indicates that older males are able to compose more variants within a given strophe type. This may indicate better learning ability and simultaneously enhance the male's competitive ability due to improved likelihood for song matching with rival males, while also making the male more attractive to females. These hypotheses would require further investigations, possibly with play-back experiments.

Our analyses also revealed that the philopatric Great Reed Warbler males had significantly larger strophe repertoires than newcomers both in terms of strophe types and variants. Great Reed Warbler females prefer both older and philopatric males (Leisler *et al.* 1995, Bensch *et al.* 1998, Hasselquist 1998, Hansson *et al.* 2004, Forstmeier *et al.* 2006, Węgrzyn *et al.* 2010), which may lead to indirect benefits such as good genes for longevity to the extent that viability is heritable (Trivers 1972, Neff & Pitcher 2005). Females may also benefit directly if older and more experienced males provide better territory, more parental help, or defence against predators (Alatalo *et al.* 1986, Marchetti & Price 1989). This may be especially advantageous in the case of philopatric males, because they are better adapted to the local social environment, i.e., they know where to find food and nesting sites, and how to avoid predators. Thus, characteristics of a given male's song may be related to age and/or philopatry and subject to direct female preference.

sentence: "Our results also showed correlations between the number of strophes (types and variants) and male's harem size. These findings suggest that females prefer larger strophe repertoires in the Great Reed Warbler. Interestingly, we earlier obtained similar results for the same species in the relationship between syllable-repertoire size and harem size (Węgrzyn & Leniowski 2010). One explanation of such similar findings may be that males that possess larger syllable repertoires are able to produce more strophe types and variants. The size of a repertoire may reflect male quality, as it has the potential to reflect early developmental stress. The so-called nutritional-stress hypothesis has been tested on nestlings of the Great Reed Warbler (Nowicki *et al.* 2000). These authors demonstrated that the length of the innermost primary feather, a standard measure of nestling development, predicted the first-year syllable-repertoire size. We believe that a similar connection exists between early development and strophe repertoire size.

Although we managed to confirm a correlation between harem size and strophe repertoire size, it was rather weak. This could be a result of small sample size, but another possibility is that the quality of a male might be assessed by females also on the basis of features other than song, such as territory quality. If this is indeed the case, song repertoires would evolve as a result of male–male competition for territories, where males use conventional communication to solve conflicts. Under intra-sexual pressure we might expect features characteristic of male–male communication, such as song sharing or song matching. In the Song Sparrow (*Melospiza melodia*), for example, song sharing enables relocation of aggressive encounters to the plane of conventional signals, where the matching between rivals' songs reflects the level of aggression (Beecher *et al.* 1996, Beecher *et al.* 2000, Beecher & Brenowitz 2005). As the song sharing increases with repertoire size up to the number of songs most common in the population, better-quality males that occupy better-quality territories are characterized by larger song repertoires. This may result in a correlation between harem and song-repertoire sizes even if there is no female preference towards larger repertoires. Whether the correlation between harem and strophe repertoire size – reported here – results from direct female preferences towards larger strophe repertoires or is indirectly linked to higher male quality needs further investigation.

4.2. Song-repertoire composition

The composition of strophe repertoire in the Great Reed Warbler was relatively stable within a season but varied considerably between seasons. During the studied three-year period, males exchanged more than half of their strophe types and almost all strophe variants. The pattern of changes in strophe types and variants indicates that males repeat some strophes in consecutive seasons but these repeats are rarely exactly the same.

The observed level of changes in strophe repertoire was similar to other open-learning species (McGregor & Krebs 1989), which suggests that the Great Reed Warbler is an "open-ended", adaptable learner. Earlier Węgrzyn and Leniowski (2010) have shown a similar pattern of changes in syllable repertoire, where the syllable composition remained stable within a season but changed significantly between years. However, between-season changes in syllable repertoire composition were much smaller than between-season changes in strophe repertoire composition. Thus, it was not clear whether the syllables considered as new had been learnt by a male or whether they were part of the individual's repertoire which had just not been used in the previous seasons. The observed high level of changes in strophe repertoire composition suggests the latter an unlikely explanation. A more plausible explanation is that males are simply able to learn and produce new strophes each season. It is also likely that older males master song composition better than younger ones, and as a result they have larger strophe repertoires.

Although our study sheds light on song organisation and learning in the Great Reed Warbler, it also brings in new questions. For example, the advantage of dropping old and composing new strophes each season remains a mystery. Another question concerns the level in which Great Reed Warbler males share their songs and use song matching for conventional male–male communication. Between-years changes in repertoire composition may enable a higher level of song sharing with neighbours or the population. The adjustment of song repertoires to population parameters across years has been demonstrated for, e.g., the Great Tit (*Parus major*; McGregor & Krebs 1989), American Redstart (*Setophaga ruticilla*; Lemon *et al.* 1994) and Sedge Warbler (*Acrocephalus schoenobaenus*; Nicholson *et al.* 2007). We believe that further research in these areas will lead to a better understanding of vocal behaviour and its function in songbirds.

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Laulun säkeiden repertuaari rastaskerttusella – järjestely, ajallinen vaihtelu ja vaikuttavat tekijät

Rastaskerttusen (*Acrocephalus arundinaceus*) koiraat laulavat reviirinpuolustuksessa ja houkutellakseen naaraita, niin ennen pesimäkautta kuin sen aikana. Tähän mennessä lajin laulua käsittelevät tutkimukset ovat keskittyneet laulun tavujen repertuaariin ja sen merkitykseen. Tässä tarkastelemme ensimmäistä kertaa rastaskerttusen laulun säkeiden repertuaaria ja järjestelyä. Analysoimme säkeiden repertuaarin laajuutta ja rakenteen muutoksia – lyhyellä ja pitkällä aikavälillä – suhteessa koiraan ikään, paikkauskollisuuteen ja haaremin kokoon. Tavut järjestäytyivät melko suureen mutta kuitenkin rajoittuneeseen valikoimaan säetyyppejä ja niiden variaatioita, joita koiras toisteli samankaltaisesti laulukauden läpi.

Pitkittäisanalyysi paljasti, että vuodenajalla ja koiraan iällä on tilastollisesti merkitsevä vaikutus säkeiden repertuaarin laajuuteen. Myös koiraan haaremikoolla oli positiivinen suhde repertuaarin laajuuteen. Säkeiden valikoima oli varsin pysyvä pesimäkauden sisällä, mutta vaihteli merkitsevästi kausien välillä. Kolmessa vuodessa koiraat vaihtoivat yli puolet säetyypeistään ja melkein kaikki säkeiden variantit. Vuosienvälinen muutos laulun säkeiden repertuaarissa viittaa siihen, että rastaskerttunen on laji, joka on sopeutunut oppimaan.

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