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Syllable sharing and changes in syllable repertoire size and composition within and between years in the great reed warbler, *Acrocephalus arundinaceus*

Ewa Węgrzyn · Konrad Leniowski

Abstract The syllable repertoire size of the great reed warbler (GRW) is known to underlay female preferences. However, its stability over a season—a key factor of this quality-related feature—has never been tested. Similarly, syllable repertoire composition, syllable sharing and its function in GRW have received little attention so far. GRW syllables fit into two categories: whistles and rattles. They differ in structure but nothing is known about their function. In the present study we analyze the above aspects of GRW vocalization. We found that syllable repertoire size and composition were stable within a season but significantly changed between years. Longitudinal analyses revealed that the changes in repertoire size were influenced more by the season than the age of individuals. The repertoire size correlated with harem size. Changes in repertoire size were significantly smaller than changes in composition, indicating varying seasonal usage of syllables present in the repertoires of individual birds. Syllable sharing was high and indifferent between neighbors and distant males. This pattern suggests that syllable sharing in GRW acts as a dialect. High levels of within- and between-season repertoire similarity among all recorded birds supported this view. Whistles were more shared and repeatable within and between seasons than rattles. We suppose that whistles may play an important role in determining a local dialect due to their lower changeability both between individuals and years. Within-season similarity of whistle repertoire to other males correlated with harem size, but similarity of rattle repertoire did not. This correlation may result from a female preference for philopatric males using the local dialect.

Keywords *Acrocephalus arundinaceus* · Song sharing · Repertoire size and composition

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Introduction

Song or syllable repertoires of many passerines are known to function in mate attraction (Anderson 1994; Reid et al. 2004) and territory defence (Hyman 2002; Brumm and Dietmar 2004), and in some species to stimulate females for reproduction (Ballentine et al. 2004; Vallet et al. 1998). There are a number of studies which demonstrate that the repertoires evolved under sexual selection, in the sense of both inter- and intrasexual pressure (Catchpole and Slater 1995; Collins 2004).

A female preference for large repertoires has been shown in laboratory experiments (Catchpole et al. 1986; Searcy 1992; Lampe and Sætre 1995) and in field studies (Catchpole 1986; Buchanan and Catchpole 1997; Mountjoy and Lemon 1996). When the size of the repertoire correlates with the male's age, this female preference for larger repertoires may lead to indirect benefits such as good genes

for longevity, to the extent that viability is heritable (Trivers 1972). Females may also benefit directly if more experienced males provide better territory, parental help, or defense against predators (Alatalo et al. 1986; Marchetti and Price 1989). However, the size of the repertoire may reflect not only the male's genetic quality but also early developmental stress. Nowicki et al. (1998) proposed that nutritional stress during the nesting period may have a negative effect on sexually selected traits, for example the size of the repertoire in adult males. This is due to a reduced learning capability resulting from poor brain development under adverse nutritional conditions. Therefore, the size of the repertoire has the potential to reflect the development of an individual. Again, if females choose males with larger repertoires, they may be provided with direct benefits from better developed males. They may also gain some indirect benefits if some individuals are more resistant to poor nesting conditions than others, and if this resistance is heritable. The nutritional stress hypothesis has been tested (among the other studies) on great reed warbler (GRW) *Acrocephalus arundinaceus* nestlings (Nowicki et al. 2000). The authors demonstrated that the length of the innermost primary feather, a standard measure of nestling development, significantly predicts first-year repertoire size. Given that nutritionally stressed males are not able to make up the size of their repertoires in following years (the GRW females prefer to pair with older males), developmental history encoded in repertoire size may explain female preference toward large repertoires.

The evolution of large repertoires driven by female choice is particularly well presented in *Acrocephalus* warblers (reviewed by Catchpole 2000). However, some studies of the GRW showed no correlation between the size of repertoire and pairing success (Forstmeier and Leisler 2004) or a stronger effect of some territory measures than the size of repertoire on paring success (Catchpole 1986). Revising results from a few previous studies (Forstmeier and Leisler 2004) showed that the strong correlation between the repertoire size of the GRW males and their pairing success was caused indirectly by covariation with male age or territory quality. After these variables had been statistically controlled for, there was no longer any significant female preference for repertoire size itself (Forstmeier and Leisler 2004).

Some further confusion arose from different results concerning the relationship between the size of the repertoire and the age of individuals. Partly this was due to different study methods (cross-sectional vs. longitudinal), but even when the same methods were used, the repertoire size depended on male age in some populations or years whereas in others it did not (Forstmeier and Leisler 2004; Forstmeier et al. 2006). Finally, some uncertainty over the function of repertoire size in female attraction arises from

the fact, that, to our knowledge, nobody has ever reported the stability of this feature in GRW males over the season. Before conducting more detailed analyses, it seems beneficial to check if the repertoire size of an individual bird is the same or different if recorded twice in the season. If it is different, the probability that it reflects male quality, his age or territory parameters will not be high.

Although the studies of the GRW are very frequently cited as evidence that song, and particularly the size of repertoire, underlies females preferences, after a closer look it is not so obvious which features of the song are preferred by females and if intersexual selection is the only pressure that shapes the song of the GRW. As the males cease after pairing (Ezaki 1987), and females pair only with intensively singing males (Catchpole 1983; Bensch and Hasselquist 1992), we may expect that the song attracts females. Whether the song feature that directs female preference is the repertoire size or a different aspect of the song, occasionally correlated with repertoire size, requires further investigation. On the other hand, the quality of a male may be assessed by a female based on features different from song, for example his territory. In this case, the GRW song would evolve as a result of male–male competition for territories. Under intrasexual pressure, we might expect features typical of male–male communication, such as song sharing. In species like song sparrow, *Melospiza melodia*, it is not the size of the repertoire but the amount of the songs shared with its neighbors that decides the male's territory tenure (Beecher et al. 2000a), which in turn is a crucial factor in the male's reproductive success (Smith 1988). As the song sharing increases with repertoire size up to the number of songs most common in the population, this may confound some findings of repertoire size correlates in species where song sharing takes place. Among the studies of the *Acrocephalus* genus, there is only one paper that analyzes song sharing in the GRW (Fisher et al. 1996), and just one that does so for the sedge warbler (Nicholson et al. 2007). In both of the studies mentioned, song sharing refers to syllable sharing, as the species are regarded as not having repeatable song strophes (Catchpole 1980, 1983). Although syllable sharing was proven in both cases, unfortunately none of the studies investigated if the males with higher syllable sharing were consequently more successful at attracting females.

In the present study we analyze the changes in the size and the composition of GRW repertoires over short (season) and long (years) periods of time, as well as the extent of syllable sharing in GRW males in a four-year study.

We also test if the size and repertoire composition (in the sense of the level of similarity between an individual male and other birds) has an effect on harem size.

The song of the GRW consists of two types of syllable: rattles and whistles repeated alternately. The two types

Fig. 1 An example of the song of the GRW and its composition
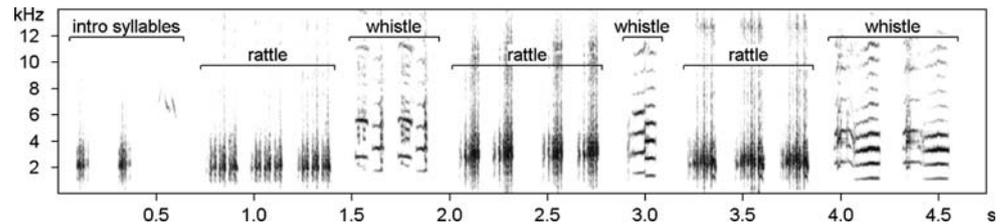
differ considerably in structure (Fig. 1), and nothing is currently known about their function in the song. Therefore, beside analyses of whole syllable repertoires, we conducted analogical procedures separately for rattles and whistles.

Materials and methods

Study area and species

The study was conducted in the years 2002–2005, from the end of April to the beginning of August. The study area consisted of ten fishponds in Korniaktów Północny near Rzeszów, south-east of Poland (50°07′20″N, 22°22′23″E). Each year 20–30 males were present within the study area, which was about 35 ha in size. The habitat of the GRW consisted of more or less patchy reed beds along the fishpond banks, with occasional shrubs and bushes. We provided almost all of the adult birds with colored rings, and nestlings with metal rings. All territories were carefully checked for nests in the years 2003–2005. We defined the size of a male's harem as the number of females that were nesting together with him (males defend the nests of their females). We measured male pairing success in terms of the number of females attracted (harem size). Male age was unknown, so to perform longitudinal analyses of changes in the size and the composition of the repertoire the males were assigned to the minimum age category of "at least 1 year old" (1+) when recorded for the first time, 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).

Recordings, bioacoustic terminology, and statistics

In previous studies of the GRW and other *Acrocephalus* warblers, "song repertoire" or "song sharing" refers to syllable repertoire and syllable sharing, as the species are not regarded as having repeatable songs (Catchpole 1980, 1983). However, during our four-year study, we observed that individuals possessed song repertoires that were quite stable within a season (Węgrzyn 2006). Therefore, in the present paper studying the vocalization of the GRW at only

the syllable level, we use the terminology of "syllable repertoire" and "syllable sharing" to avoid confusion with the results of other publications investigating song repertoires in the GRW.

We analyzed the sizes and the detailed compositions of the syllable repertoires of 15 males each year on average (range = 9–21). Sixteen males were recorded twice during the season (8 in 2004 and 8 in 2005), and we used these recordings to evaluate changes in the syllable repertoire size and composition over short time. For longitudinal analyses, we used recordings of returning males ($n = 15$). We recorded two males for all four seasons, five males for three seasons, and eight males for two seasons. In a particular season, each male was continuously recorded for at least 10 min during a single session, and most were recorded for 30 min. Males were recorded from a distance of 2–4 m. All recordings were made with an AKG C568 EB shot-gun microphone and a Sony MZR 50 Mini Disc player. Sonograms were analyzed using the current version of Avisoft SASLab Pro 4.x.

Syllable repertoire size and composition was estimated on the basis of 10 min samples of continuous singing (most GRW males will present their full syllable repertoire within this time period, as presented in the "Results"). A syllable library for each individual male was created by visually inspecting sonograms. Syllables were defined as the smallest unit of continuous song (Catchpole 1980). We calculated the changes in syllable repertoire size for a particular male using the formula $1 - R'/R''$, where R' is the smaller repertoire size and R'' is the larger repertoire size derived from the two different recordings of the same bird (R'/R'' is the similarity in size of the two recordings). To calculate the changes in syllable repertoire composition for a particular male, we used the formula: $1 - 2N_s/(R_1 + R_2)$, where N_s is the number of same syllables, and R_1 and R_2 are the repertoire sizes from the two different recordings of the same male ($2N_s/(R_1 + R_2)$ is the similarity in composition of the two recordings). In analyses of short time changes, we used recordings of the same bird separated at least by six days. To analyze long-term changes, we used recordings of the same males from different seasons (longitudinal analyses). We separately calculated changes that occurred over two, three and four seasons. To test the effects of age and season on the changes in syllable repertoire, we used linear mixed model

analysis with male as a subject, repertoire size as a dependent variable, and age and season as factors.

To calculate the proportion of syllable types shared between two individuals, the syllable repertoire libraries of males were compared by visual inspection. We calculated syllable sharing using the formula $2N_s/(R_1 + R_2)$, where N_s is the number of shared syllables and R_1 and R_2 are the repertoire sizes of the two individuals (McGregor and Krebs 1982). Syllable sharing was calculated separately for pairs of neighbors (16 pairs: eight from 2004 and eight from 2005) and randomly chosen distant birds (16 pairs: eight from 2004 and eight from 2005). Because we found out that there are some changes in the compositions of individual GRW male repertoires within a season, we wanted to know if the neighbors actively adjust the compositions of their repertoires to each other. We assumed that if they do so, syllable sharing should be higher for recordings of neighbors from the same day than when separated in time. Therefore, we calculated the song sharing of neighbors using recordings from the same day (16 pairs) and from different days (14 pairs). Recordings from different days were separated in time by at least seven days. Territories of neighbors were mostly adjacent to each other or were separated by up to 20 m of reeds, and we saw males interacting frequently. Territories of distant birds were located on different fish ponds; the birds did not hear each other and did not interact directly. Territories were 200–800 m apart.

We also calculated the within-season similarity in composition of individual bird repertoires between birds recorded within the same season; in other words, syllable sharing between the bird and the rest of the population. The difference between this approach and the previously calculated syllable sharing is that syllable sharing reveals the proportion of syllable types shared between two individuals, while within-season similarity shows the mean proportion of syllable types shared by the male with all other males. To do this, we created a matrix of similarities (based on Euclidian distances, Jaccard correlation) for all birds recorded during a given season (2002, 2003, 2004 and 2005), and then calculated a mean value of similarity for each bird as well as the mean similarity of all birds within a season.

Finally, we analyzed if there are seasonal trends in the use of particular sets of syllables by most of the males, or if the repertoire syllable composition is stable across years. We calculated the mean between-season similarity (similarity in the syllable repertoire of each bird to that of all birds from different seasons) using a matrix of similarity (based on Euclidian distances, Jaccard correlation) for all birds from the four seasons pooled together (2002–2005). We used recordings of returning birds in one season only (to avoid pseudoreplication if the repertoire composition of

returning males is dependent on what they sung in the previous season). We assumed that if there are seasonal "fashions" for particular sets of syllables, the between-season similarity calculated for years 2002–2005 should be significantly lower than the mean value of the within-season similarity in 2002, 2003, 2004 and 2005.

To test the effect of repertoire size and composition on male harem size, we used Spearman's rank correlation. We used data from the 2003–2005 seasons, as we lacked harem size records for 2002. We analyzed the effects for separate seasons and for the three seasons pooled together. In the latter analyses, we calculated correlations in two ways: we treated each male in given season as an independent statistical unit (i.e., in the case that returning males are free to compose their repertoires independently of what they sung in the previous season, and/or the condition of particular male can differ significantly every season), and we used recordings of returning birds in one season only to avoid pseudoreplication (i.e., if the repertoire and condition of a male is correlated to its repertoire and condition from the previous season).

All of the above analyses carried for whole repertoires were also conducted separately for rattles and whistles, as we were interested in whether the two different types of syllables undergo similar or different changes.

All of the statistical analyses described above were conducted using SYSTAT, SPSS and Statistica.

Results

Syllable repertoire size and composition

The song of a GRW male contains a few introductory syllables followed by whistles (tonal syllables) and rattles (noisy syllables) repeated alternately (Fig. 1). Whistles are characterized by a narrow-banded frequency that is modulated in time and has a number of harmonics. The syllables usually have two elements. Rattles consists of many short elements with a wide frequency band and fast repetition.

Syllable repertoire size and composition were estimated based on 10 min samples of continuous singing, as within this time the majority of the GRW males present their full syllable repertoire (Fig. 2).

The mean size of the syllable repertoire in the studied population was 40.1 (min = 26, max = 51, SE = 1.05, $n = 38$). On average, the syllable repertoire was composed of 42% whistles and 58% rattles (Fig. 3). The mean size of a whistle repertoire was 16.7 (min = 12, max = 21, SE = 0.35, $n = 38$) and that of a rattle repertoire was 23.4 (min = 13, max = 31, SE = 0.76, $n = 38$).

Short-term changes in syllable repertoire size and composition

To evaluate changes in syllable repertoire size and composition for the same male over a short time, we used the recordings for 16 males that were recorded twice during the season. Recordings of the same bird were separated at least by 6 days. The detailed changes in size and composition of the GRW syllable repertoire observed within a season are presented in Table 1.
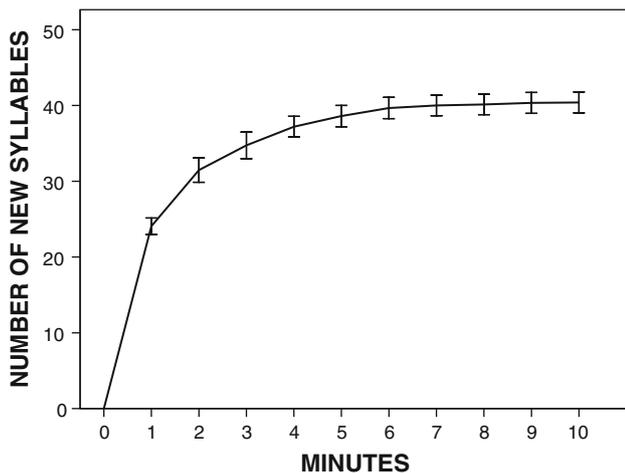

Fig. 2 Average number of new syllable types versus consecutive minutes of singing ($n = 38$ males). The *bars* show SEs

Repertoire size changes

The size of the syllable repertoire remained relatively constant over a short time (Fig. 4). Changes in the sizes of the repertoires of whistles and rattles were similar. The changes in repertoire size were not directional—in eight cases syllables were dropped, in five cases males gained new syllables, and the repertoire sizes of three birds remained unchanged.

Repertoire composition changes

The composition of the syllable repertoire for each individual also remained relatively constant within a season (Fig. 4). However, the changes in the compositions of whistles and rattles were not proportional. Changes in the composition of the rattle repertoire ($\overline{X} = 14\%$) were significantly higher than changes in the composition of the whistle repertoire ($\overline{X} = 5\%$) (Wilcoxon signed-rank exact test: $Z = 3.31$, $N = 16$, $P < 0.001$), indicating that the whistle repertoire is more stable within a season.

Long-term changes in syllable repertoire size and composition

To evaluate changes in the syllable repertoire size and composition for the same male over a period of years, we used recordings of returning males. We recorded two males across all four seasons, five males across three seasons, and eight males across two seasons. The changes in size and
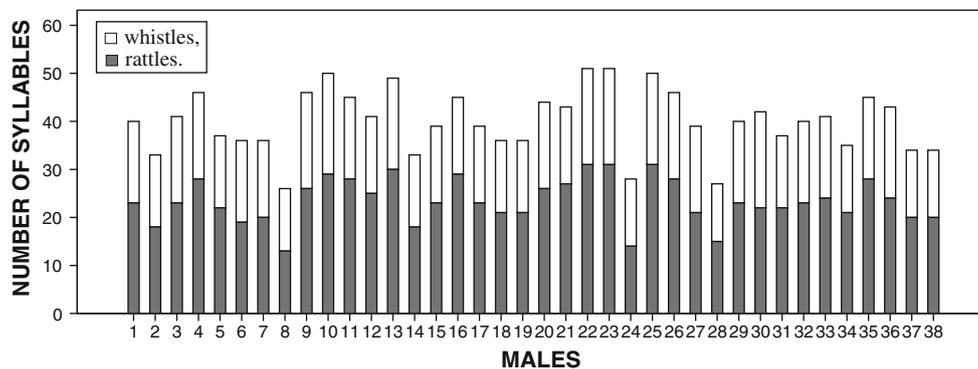

Fig. 3 Syllable repertoire size and distribution of whistles and rattles in songs of different males ($n = 38$). *Open squares*, whistles; *filled squares*, rattles

Table 1 Changes in size and composition of the GRW syllable repertoire within a season, $n = 16$

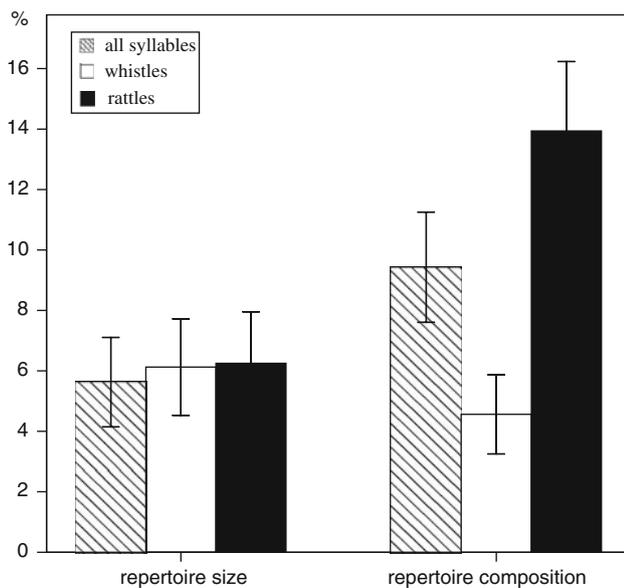| Changes in syllable repertoire size (%)									Changes in syllable repertoire composition (%)								
All of the repertoire			Whistles			Rattles			All of the repertoire			Whistles			Rattles		
$\overline{X}$	Min–max	SE	$\overline{X}$	Min–max	SE	$\overline{X}$	Min–max	SE	$\overline{X}$	Min–max	SE	$\overline{X}$	Min–max	SE	$\overline{X}$	Min–max	SE
6	0–20	1.5	6	0–21	1.6	6	0–25	1.7	10	1–28	1.7	5	0–19	1.3	14	0–40	2.3

Fig. 4 Within-season changes in GRW syllable repertoire size and composition (*n* = 16). The *bars* show SEs. The graph presents the changes estimated for all syllables (*hatched squares*), whistles (*open squares*), and rattles (*filled squares*) separately

time (1, 2 and 3 years), but the differences were statistically insignificant. Although the mean change in size of the rattle repertoire was higher than that of the whistle repertoire, the differences were also insignificant.

To study the pattern of changes in syllable repertoire size between seasons, we conducted two kinds of longitudinal analyses. First, we assigned all returning males to minimum age categories (1+, 2+, 3+ and 4+), as the true ages of all males were unknown. In year 1+, syllable repertoire sizes ranged from 21 to 46; in year 2+ they ranged from 41 to 52; in year 3+ from 42 to 53; and in year 4+ from 41 to 47. Second, we assigned all returning males to the seasons in which they were recorded (2002, 2003, 2004 and 2005). The effect of age and season on repertoire size was analyzed using a linear mixed model (Table 3). This showed that there was significant effect of season on syllable repertoire size (*F* = 6.7, *P* = 0.006) and an almost significant effect of age (*F* = 5.08, *P* = 0.053). As there was no significant interaction between age and season, the result shows that there are seasonal variations in syllable repertoire size that are unrelated to the age of the individual.

Cross-sectional analyses of syllable repertoire size in seasons 2002–2005 in the studied GRW population also revealed seasonal variations in the mean number of syllables and supported the results of longitudinal analyses (Fig. 6).

composition of the GRW syllable repertoire between seasons are presented in Fig. 5, and the precise values of these changes are given in Table 2.

Repertoire size changes

The changes in syllable repertoire size between two seasons were significantly higher than the changes within a season (Mann–Whitney *U* test: *Z* = 3.3, *P* = 0.014, n_1 = 14, n_2 = 16). Repertoire size changes increased with

Repertoire composition changes

The changes in the syllable repertoire composition between two seasons were significantly higher than the changes within a season (Mann–Whitney *U* test: *Z* = 4.2, *P* < 0.001,
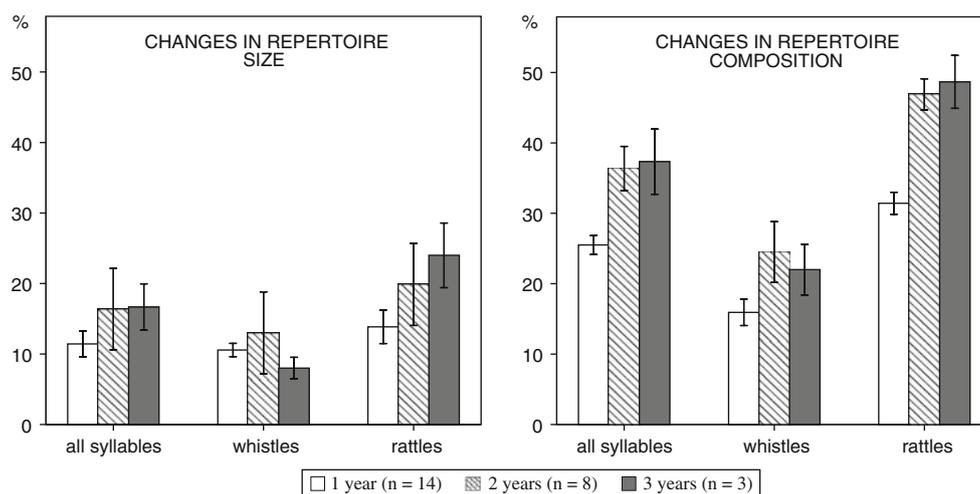

Fig. 5 Long-term changes in syllable repertoire size and composition. The *bars* show SEs. The graph presents the changes estimated for all syllables, whistles and rattles separately. The changes were

counted over time intervals of: *open squares*, 1 year (*n* = 14); *hatched squares*, 2 years (*n* = 8); *filled squares*, 3 years (*n* = 3)

Table 2 The changes in GRW syllable repertoire size and composition between seasons

| | Changes in syllable repertoire size (%) | | | | | | | | | Changes in syllable repertoire composition (%) | | | | | | | | |
| | All syllables | | | Whistles | | | Rattles | | | All syllables | | | Whistles | | | Rattles | | |
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
TI	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
$\overline{X}$	11	16	17	11	13	8	14	20	24	25	36	37	16	25	22	31	47	49
Min–max	2–25	0–50	12–23	6–15	0–50	6–11	0–32	4–50	18–33	16–34	26–56	29–45	9–30	12–53	17–29	20–38	40–58	42–55
SE	1.8	5.8	3.2	3.5	5.8	1.5	2.4	5.8	4.6	1.3	3.1	4.6	1.9	4.3	3.6	1.6	2.2	3.8
n	14	8	3	14	8	3	14	8	3	14	8	3	14	8	3	14	8	3

1, 1 year; *2*, 2 years; *3*, 3 years

TI, time interval between recordings; *n*, number of individuals in the longitudinal analysis

Table 3 The effects of age and season on repertoire size (LMM; type III tests of fixed effects)

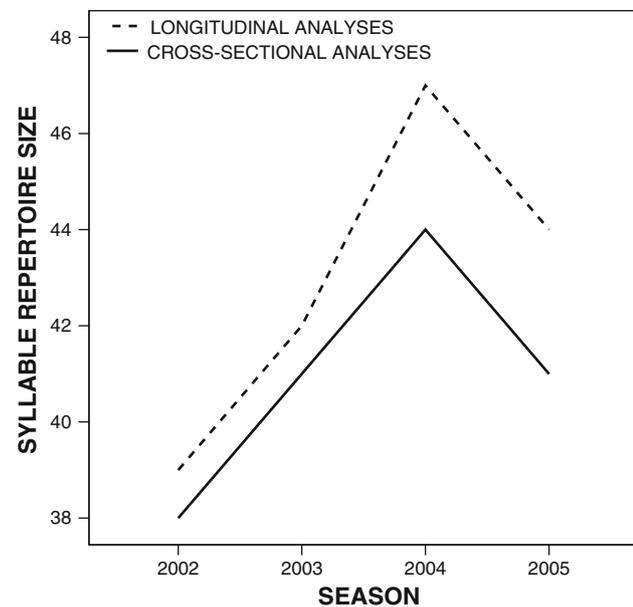| Source	Numerator (*df*)	Denominator (*df*)	F	Sig.
Intercept	1	12,873	3489.189	0.000
Age	3	5,335	5.084	0.053
Season	3	12,944	6.699	0.006
Age × season	2	8,257	1.604	0.258

Dependent variable: repertoire

Fig. 6 Longitudinal ($n = 15$) and cross-sectional ($n = 39$) analyses of mean syllable repertoire size for seasons 2002–2003

$n_1 = 14$, $n_2 = 16$). Repertoire composition changes were significantly greater for a 2-year compared to a 1-year time interval ($Z = 3.1$, $P = 0.002$, $n_1 = 14$, $n_2 = 8$) but not for a 2-year compared to a 3-year time interval. This shows that the changes are not due to the addition of new syllable types each year, but rather to different seasonal usages of the syllables present in the repertoires of individual birds. This result is consistent with the pattern of changes in

syllable repertoire size, which also undergoes seasonal variations. The changes in whistle repertoire composition were significantly smaller than the changes in rattle repertoire composition ($Z = 3.95$, $P < 0.001$ for a 1-year time interval, $Z = 2.67$, $P = 0.007$ for a 2-year time interval, $Z = 1.96$, $P = 0.05$ for a 3-year time interval). This difference is especially pronounced at longer time intervals; e.g., after 3 years the mean change in whistle repertoire was 22% while the mean change in rattle repertoire was 49% (Table 2).

Long-term changes in repertoire size and composition were not proportional (Fig. 5): changes in size were significantly smaller than changes in composition for both the 1- and 2-year time intervals (Wilcoxon signed-rank exact test: $Z = 3.23$, $N = 14$, $P < 0.001$, $Z = 2.52$, $N = 8$, $P < 0.001$).

Syllable sharing between neighboring and distant males

The rate of syllable sharing in the studied GRW population was high and unrelated to either the date of recording or the male's location (Fig. 7).

Neighboring males recorded on the same day shared between 58 and 91% ($\overline{X} \pm SE = 77 \pm 2.7\%$, $n = 16$ pairs) of their syllable repertoires. Sharing of whistles varied between 62 and 92% ($\overline{X} \pm SE = 82 \pm 2.4\%$), and sharing of rattles varied from 51 to 93% ($\overline{X} \pm SE = 74 \pm 3.4\%$). Whistles were shared significantly more than rattles (Wilcoxon signed-rank exact test: $Z = 2.92$, $N = 16$, $P = 0.001$). In "Syllable repertoire size and composition," we demonstrated that there was a mean 10% change in repertoire composition for an individual within a season. To test whether neighbors actively adjust their repertoire composition in order to enhance syllable sharing, we calculated syllable sharing for the same pairs of neighbors recorded on different days.

Neighboring males recorded on different days (time interval at least 6 days) shared between 62 and 90% of their syllables ($\overline{X} \pm SE = 78 \pm 3.0\%$, $n = 14$ pairs), which was very similar to the level of syllable sharing noted on
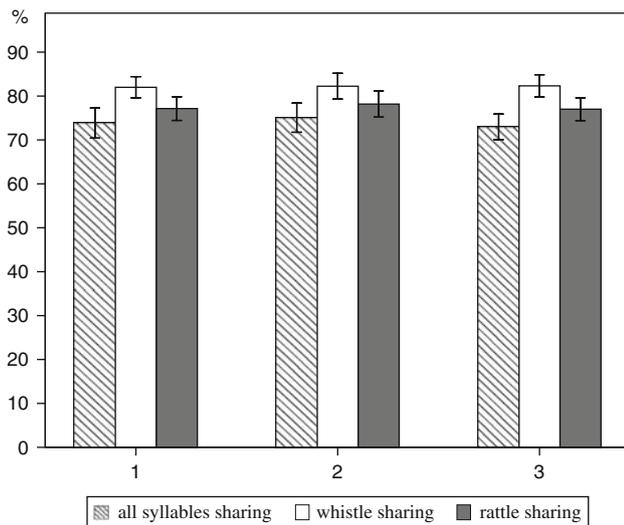
Fig. 7 Syllable sharing in the GRW. *1*, Neighboring males recorded on the same day; *2*, neighboring males recorded on different days; *3*, distant males; *hatched squares*, all-syllable sharing; *open squares*, whistle sharing; *filled squares*, rattle sharing. The *bars* show SEs

the same day (Mann–Whitney *U* test: $Z = 0.2$, $P = 0.8$). This shows that neighboring males do not adjust their repertoire compositions to each other. Sharing of whistles varied between 62 and 97% ($\overline{X} \pm SE = 82 \pm 3.0\%$), and sharing of rattles varied between 57 and 91% (($\overline{X} \pm SE = 75 \pm 3.3\%$). Whistles were shared significantly more than rattles (Wilcoxon signed-rank exact test: $Z = 2.36$, $N = 12$, $P = 0.02$).

Distant males shared similar amounts of syllables to those shared by neighbors (Mann–Whitney *U* test: $Z = 0.57$, $P = 0.57$), which was quite an unexpected result. Syllable sharing between non-neighbors varied from 61 to 86% ($\overline{X} \pm SE = 77 \pm 2.6\%$, $n = 16$ pairs). Whistle sharing was between 67 and 89% ($\overline{X} \pm SE = 82 \pm 2.5\%$), and rattle sharing between 56 and 84% (($\overline{X} \pm SE = 73 \pm 2.9\%$). Again, sharing of whistles was significantly higher than sharing of rattles (Wilcoxon signed-ranks exact test: $Z = 3.52$, $N = 16$, $P < 0.000$).

Similarity in syllable repertoire composition for GRW males within a season and between years

In "Long-term changes in syllable repertoire size and composition," we demonstrated that the syllable repertoire compositions of individual males changed between years, and in the previous section we demonstrated that there was a high level of syllable sharing between the GRW males within a season irrespective of their locations and recording dates. Here we analyze the similarity in repertoire composition among all males recorded within a particular

season, as well as the similarity in repertoire composition between males from different years (Fig. 8).

The aim of this approach was to test whether there are seasonal singing fashions that are followed by most of the males present in given area, or if the repertoire composition is stable between years at the population scale.

Within-season similarity

The mean similarity in syllable repertoire composition for males recorded within a single season was 63%, the mean similarity in whistle repertoire was 71%, and that for the rattle repertoire was 58% (Fig. 8). For all of the seasons, the similarity in whistle repertoire among the males was significantly higher than the similarity in rattle repertoire (Wilcoxon signed-rank exact test: $Z = 2.67$, $N = 9$, $P = 0.008$, $Z = 4.02$, $N = 21$, $P < 0.001$, $Z = 3.41$, $N = 15$, $P < 0.001$ and $Z = 3.62$, $N = 17$, $P < 0.001$, respectively, for seasons 2002, 2003, 2004 and 2005). This pattern strongly resembles the pattern of syllable sharing observed for pairs of birds in "Syllable sharing between neighboring and distant males," and it explains why the level of song sharing did not differ between neighbors and distant birds—in the studied population, all of the males obviously used a similar set of syllables within a season.

Between-years similarity

The mean similarity in syllable repertoire composition for males recorded in different years was 49%, the mean similarity in whistle repertoire was 62%, and that for the rattle repertoire was 41% (Fig. 8). The similarity in whistle
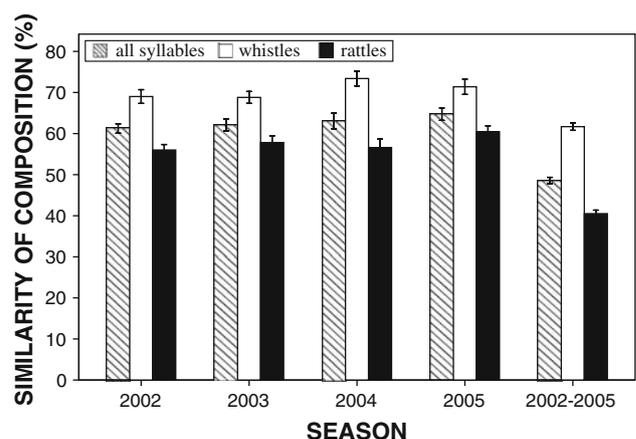

Fig. 8 Similarity in repertoire composition in GRW males. Within-season similarity: 2002 ($n = 9$), 2003 ($n = 15$), 2004 ($n = 21$) and 2005 ($n = 17$). Between-years similarity: 2002–2005 ($n = 38$). The *bars* show SEs. *Hatched squares*, all syllables; *open squares*, whistles; *filled squares*, rattles

repertoire among the males was significantly higher than the similarity in rattle repertoire (Wilcoxon signed-rank exact test: $Z = 5.37$, $N = 38$, $P < 0.001$).

The similarity in repertoire between males from different years (mean 49%) was significantly lower than that between males recorded during the same season (mean: 63%) (Mann–Whitney U test: $Z = 8.37$, $P < 0.001$). This result supports what we showed in "Long-term changes in syllable repertoire size and composition" for the longitudinal analyses—the syllable repertoire compositions of GRW males in the same breeding area change every year, but the whistle repertoire changes significantly less than the rattle repertoire.

Effects of syllable repertoire size and composition on harem size

Correlations between syllable repertoire size and harem size were not statistically significant when calculated for separate seasons. However, when we used pooled data from three seasons (2003–2005), the correlation became significant (Spearman's rank correlation: $R = 0.28$, $N = 53$, $P = 0.021$). The size of the whistle repertoire was slightly more correlated with harem size than size of rattle repertoire ($R = 0.35$, $P = 0.006$ and $R = 0.27$, $P = 0.028$, respectively). When we used recordings of returning birds in one season only (to avoid pseudoreplication), the correlation became even stronger (Spearman's rank correlation: $R = 0.54$, $N = 35$, $P < 0.001$ for all of the repertoire, $R = 0.55$, $N = 35$, $P < 0.001$ for whistles, and $R = 0.48$, $N = 35$, $P = 0.002$ for rattles).

Similarity in the repertoires of individual birds to those of other birds within a season showed no significant effect on harem size when calculated for separate seasons. An analysis of pooled data from three seasons (2003–2005) revealed a significant effect of whistle repertoire similarity on harem size (Spearman's Rank Correlation: $R = 0.26$, $N = 53$, $P = 0.03$). The effects of similarity in rattle repertoire and similarity in whole-syllable repertoire on harem size remained insignificant. Upon using recordings of returning birds in one season only, the correlation between whistle repertoire similarity and harem size became stronger (Spearman's rank correlation: $R = 0.35$, $N = 35$, $P = 0.03$), while the effects of similarity in rattle repertoire and similarity in whole-syllable repertoire on harem size were still insignificant.

We also tested whether similarity in the repertoire of an individual bird to the repertoires of birds from different seasons is correlated with harem size. Unexpectedly, this effect was greater than the effect of similarity in the repertoire of an individual bird to those of other birds within a season (Spearman's rank correlation: $R = 0.4$, $N = 35$, $P = 0.009$ for all repertoire, $R = 0.42$, $N = 35$,

$P = 0.006$ for whistles and $R = 0.35$, $N = 35$, $P = 0.019$ for rattles).

Discussion

Changes in repertoire size and composition over time

We found that syllable repertoire size and composition were relatively stable within a season, but that both features significantly changed between years. Both longitudinal and cross-sectional analyses revealed a similar pattern of seasonal variation in the mean number of syllables, with the largest repertoires noted in the year 2004. When we entered both age and season into longitudinal analyses, the results showed a significant effect of season and an almost significant effect of age of the individual on syllable repertoire size, which means that differences between the repertoire sizes of individuals were higher between seasons than between age categories. As there was no significant interaction between the age and the season, this result shows that there are seasonal variations in syllable repertoire size that are unrelated to the age of the individual. Cross-sectional analyses supported this view. This is the first study that shows directional seasonal variations in the size of the syllable repertoire among all of the GRW males involved in analyses. Previous papers concerning the relation between syllable repertoire size and male age have given mixed results (Forstmeier and Leisler 2004; Forstmeier et al. 2006). It is possible that repertoire size depends on male age in some GRW populations but not in others. Another possibility is that the effect of age (or the lack of such an effect) reported in cited studies may have been due to positive or negative coincidence with seasonal variations in repertoire size that are caused by factors independent of age. If our study had only included seasons 2002–2004, the analysis would have shown a positive effect of age on repertoire size, while no effect of age would have been observed for seasons 2003–2005, and analyses conducted only for the years 2004–2005 would have indicated a negative effect. Another possible problem with longitudinal analyses of age-dependent variables (i.e. repertoire size) is that the exact age of an individual is often unknown, so males are classified into minimum age categories: 1+, 2+, etc., which represent the first year of observing a male in a given study area but not its real age. Consequently, there may be unpredicted proportions of individuals of very different real ages in every age category. If the analyses show continuous and proportional increases in repertoire size in subsequent age categories, this in fact means that repertoire increases with age during the life spans of individuals. However, the connection between age and repertoire size does not seem as clear if,

for example, the largest increase in repertoire is reported between the first and the second age category (1+ and 2+), which really means between the first and the second year that the individual was observed. Such a relationship between age and repertoire size was demonstrated for example in the sedge warbler (Nicholson et al. 2007). As individuals aged (i.e., time since first spotted or ringed) 1+ years may be either young or old, this raises the question of what makes them increase their repertoires by a notably greater degree during the second year of observation than during any other? If we studied real ages, we would be able to say that younger birds increase their repertoire sizes more than older ones. However, with age categories, which may contain birds of all possible ages, we cannot say this. We suggest that some relations that are reported as being age dependent may in fact be found to be season dependent where the analyses were conducted on relative age categories. It may be worth entering "season" in addition to "age" into such analyses in order to see which of them has a stronger effect on the dependent variable, for example the size of the repertoire.

The question of which of the factors may have caused seasonal variations in repertoire size in our study remains. Unfortunately, we were not able to control all variables in the study area, such as the exact number of females (for example, the second female of a polygynist may have been a female that deserted another male after nest predation) or the weather conditions. However, we perceived the year 2004 as being extremely tough due to low temperatures in May, as well as the occurrence of heavy rains and winds that made data collection and song recording difficult. It is possible that this adverse weather affected the birds too, as it was the only season in which we regularly found one or two dead chicks in nests, probably due to starvation. After heavy rains, some nests were so soaked that they slid down the reeds and sank with the eggs or nestlings. We also observed that some renesting females built "roofed" nests, situating their newly constructed nests under abandoned/predated nests or in dense bushes, which we interpreted as a reaction to adverse weather conditions. Nest losses, if connected with male desertion, may have increased competition for females and thus resulted in repertoire size enlargement. Another factor that caused the seasonal increase in repertoire size may have been the number of new males joining the philopatric population. We demonstrated that the GRW males tend to share a considerable proportion of their repertoires, so newcomers may enrich "the local repertoire" with new syllables, given that the GRW adult males are able to learn new syllables, and that local and new male repertoires differ in composition. Although there is a lack of information on GRW learning strategies and dialects, we consider the last explanation to be quite unlikely, as we

also observed (and ringed) newcomers in 2005, when the mean repertoire size decreased.

As increasing the repertoire obviously involves adding new syllables, it is often interpreted that birds that increase the sizes of their repertoires over time are open learners. However, the syllables that are considered new by researchers may actually already belong to the bird's repertoire, but they were just unused in the previous season or two. The decrease in repertoire size in 2005 shown by our longitudinal analyses reveals that the GRW males do not necessarily present all of the syllables they know during each season. Further support for such a mechanism comes from our analyses of between-years changes in syllable repertoire composition. The average change in composition between any two consecutive seasons (1-year time interval) was 25%. If these composition changes were due to the addition of new syllables, we might expect a 50% change over a 2-year interval and a 75% change over 3 years. This was not the case, as the composition changes obtained in the longitudinal analyses were 36 and 37% respectively, indicating that these changes are not due to the addition of new syllable types each year, but are instead due to changes in the usage of the syllables present in repertoires of individual birds between seasons. Additionally, long-term changes in repertoire size and composition were not proportional: changes in size were significantly smaller than changes in composition for both 1- and 2-year time intervals. This observation suggests that GRW males rotate a considerable fraction of the syllables they sing each season.

Syllable sharing and composition similarity

Numerous studies have investigated song sharing in birds (Vehrencamp 2000). A general pattern of song or syllable sharing involves having more elements in common with neighbors than non-neighbors (McGregor and Krebs 1982, 1989, Grießmann and Naguib 2002). The results of our study differed from this pattern, as we found that the amount of syllables shared between neighbors and distant males was very similar (mean of 77% in both cases). We know of only one other paper that studied song sharing in the GRW: Fisher et al. (1996) showed a similarly high rate of mean syllable sharing (79%, $n = 10$) and a weak negative correlation between the rate of syllable sharing and the distance between the males' territories. Unfortunately, the study area and the distances between territories are not given, so it is difficult to say whether the lack of such a correlation in our study is due to different distances between pairs of non-neighbors or a different pattern of syllable sharing in the two populations. Our results surprised us all the more, as sedge warbler (*Acrocephalus schoenobaenus*), a species that is closely related to the

GRW, demonstrates the typical pattern of sharing more syllable types with its nearest neighbors than with males that are further away (Nicholson et al. 2007). Also, the average syllable sharing in the sedge warbler is much lower than in the GRW (37% between neighbors, and 19.5% between distant males), and sedge warbler neighbors increase their syllable sharing as the time spent singing together increases, which is not the case for the GRW. These inconsistent results from the studies of related and often sympatric species made us consider whether syllable sharing may serve different functions in different species, resulting in different patterns. In species like the song sparrow (*Meulospiza melodia*), song sharing enables the relocation of aggressive encounters to the plane of conventional signals, where the level of matching between rivals' songs reflects the level of aggression (Beecher et al. 1996; Beecher et al. 2000b; Beecher and Brenowitz 2005; Beecher and Campbell 2005). Thus, sharing a proper number of songs with neighbors is crucial to effective male–male competition and territory tenure (Wilson et al. 2000; Beecher et al. 2000a), which in turn decides male lifetime reproductive success (Smith 1988). In this scenario, song sharing with the nearest neighbors is of great importance, as interactions with them are the most common. This relation leads to disproportionate levels of song sharing with close and distant birds. However, song sharing, which means that the repertoires of both birds have a number of the same or similar songs, does not have to translate into song matching. It may just cause a local dialect if the level of sharing is high enough among a majority of individuals. The function determines the pattern of song sharing, as within the range of a dialect, most of the individuals are expected to share a high number of vocalization elements irrespective of how often they directly interact. On the other hand, dialect does not exclude song matching in territorial interactions, so in theory both functions of song sharing can be met simultaneously, with the reservation that the presence of the dialect diminishes the differences between the level of song sharing between neighbors and non-neighbors. Our results suggest that the syllable sharing observed in the GRW serves as a dialect. Whether conventional communication (in the sense of syllable or song matching) also takes place in GRW males requires further investigation and analyses of simultaneous recordings of singing neighbors. An alternative explanation for the lack of difference in syllable sharing between neighbors and distant birds is that all of the individuals may have had the chance to listen to other males while foraging outside of their territories. We cannot fully reject this possibility, as we observed males leaving their territories during singing breaks, and we also sometimes mist-netted individuals some distance from their territories. As the study area was about 30 ha, and singing

breaks are typically 15–20 min, males were theoretically able to visit all other singing individuals. However, if syllable sharing serves conventional communication through song matching, we should still expect a higher level of syllable sharing with neighbors due to more frequent direct interactions between them.

The view that syllable sharing functions as a dialect in the GRW males is also supported by the observation of relatively high levels of within-season (63%) and between-season (49%) repertoire similarities in all recorded birds. The lower between-season similarity suggests that there are seasonal fashions in repertoire composition that are followed by most of the birds. As the mean between-season changes in repertoire size rarely exceed a few syllables, and the composition can change by half, we assume that the birds do not use their full syllable repertoires each season, or alternatively that they learn new syllables each year and forget the old ones, which seems less likely. The conclusions from analyzing within- and between-season similarities at population scale are very coincident with what we found in longitudinal analyses of repertoire composition and size, and they support the model of the partial use of the full syllable repertoire during a single season.

Effects of syllable repertoire size and composition on harem size

We only found a correlation between repertoire size and male harem size when analyzing pooled data from three seasons. We suppose that the lack of the correlation for single seasons was mainly due to the sample size, as the trend was positive for all single seasons. We demonstrated that the syllable repertoire size of an individual was stable within a season, so it may be a reliable signal of the male's quality or the quality of a feature connected with the male, such as his territory. The correlation between syllable repertoire size and harem has also been presented in previous studies on the GRW (Catchpole 1986; Hasselquist 1994, 1998). However, in some cases, when age was entered into analyses as a covariate it showed a stronger effect on harem size than repertoire size per se (Forstmeier and Leisler 2004; Forstmeier et al. 2006). Our analyses indicate that there was stronger effect of season than age on the syllable repertoire size. This suggests that males, irrespective of their ages, are able to respond to some— probably environmental—factors by increasing their repertoire sizes, and that females may prefer males with larger syllable repertoires for reasons other than their ages.

Interestingly, harem size was significantly correlated with similarity in repertoire composition to birds from different seasons, indicating that females may favor conservative repertoires that allow them to recognize

philopatric males. A female preference for philopatric males was presented by Bensch et al. (1998), but the cue used to recognize the returning male was never studied for the GRW. With respect to the within-season similarity of a male's repertoire to those of the other birds, the only aspect of repertoire composition that was correlated to harem size was similarity in whistle repertoire. We suppose that whistles may be more important for determining the dialect. We discuss this in the next section.

Whistles and rattles

The considerably different structures of whistles and rattles combined with the frequent use of both elements in GRW vocalization raises a question about their function.

The composition of the whistle repertoire of an individual bird was more stable both within and between seasons. The difference between the changes in whistles and rattles were especially pronounced at longer time intervals; e.g., after 3 years the mean change in whistle repertoire was 22%, but the repertoire of rattles had changed by 49%. Whistles were also shared significantly more than rattles, between both neighbors and distant birds. This pattern continued when we analyzed the similarity in the repertoire compositions of all recorded birds within and between seasons: the similarity in whistle repertoire among the males was significantly higher than the similarity in rattle repertoire. Our results demonstrate that whistles are a more conservative element of the GRW song than rattles. We suppose that whistles may play an important role in determining the local dialect due to their lower change-ability across both individuals and years. Similarity in the whistle repertoire of an individual bird compared to those of other birds within a season was correlated with harem size, while there were no effects of similarity in rattle repertoire and similarity in whole-syllable repertoire on male harem. If whistles indicate the local dialect, this may explain the female preference for individuals with a higher number of whistles that are shared with other males.

The possible role of whistles as dialect markers requires further investigation involving studies of populations that are separated by considerable distances.

Zusammenfassung

Veränderung der Größe des Elementrepertoires, der Komposition und bei gemeinsamen Elementen innerhalb einer Brutsaison und zwischen Jahren im Drosselrohrsänger, *Acrocephalus arundinaceus*

Die Größe des Elementrepertoires im Drosselrohrsänger unterliegt der Auswahl durch Weibchen. Obwohl es ein

qualitätsabhängiger Schlüsselfaktor ist wurde die Stabilität der Repertoiregröße während der Brutsaison nie getestet. Ebenso wenig Aufmerksamkeit wurde dem Elementrepertoire, dem Auftreten gemeinsamer Elemente und deren Funktion gewidmet. Die Gesangselemente des Drosselrohrsängers können in zwei Kategorien unterschieden werden: Pfiffe und Knattern. Diese unterscheiden sich in der Struktur, jedoch ist über ihre Funktion nichts bekannt. In der vorliegenden Arbeit haben wir Aspekte des Gesanges beim Drosselrohrsänger untersucht. Während einer Brutsaison waren die Größe des Elementrepertoires und die Komposition stabil, zwischen verschiedenen Jahren wurden jedoch signifikante Unterschiede gefunden. Eine Langzeitstudie zeigte dass diese Veränderungen in der Größe des Repertoires stärker von der Brutsaison als von dem Alter der Individuen bestimmt wurden. Die Größe des Repertoires korrelierte mit der Größe des Harems. Veränderungen in der Repertoiregröße waren signifikant geringer als Veränderungen in der Komposition, was auf saisonal wechselnde Verwendung vorhandener Elemente im Repertoire eines individuellen Vogels hinweist. Gemeinsame Elemente waren vorhanden und sie variierten nicht zwischen Nachbarn und weiter entfernt brütenden Männchen. Dies lässt vermuten dass Elementsharing im Drosselrohrsänger möglicherweise einen Dialekt darstellt. Während und zwischen Jahren waren die Repertoire aller aufgenommenen Vögel relativ ähnlich. Dies unterstützt die Annahme eines Dialektes. Pfiffe waren reproduzierbar und wurden häufig gemeinsam benutzt. Möglicherweise spielen Pfiffe, aufgrund ihrer geringen Variabilität zwischen Individuen und Jahren, bei der Bestimmung des lokalen Dialektes eine wichtige Rolle. Innerhalb einer Brutsaison war die Ähnlichkeit des Pfiffrepertoires relativ zu anderen Männchen korreliert mit der Haremgröße, die Ähnlichkeit des Knatterrepertoires jedoch nicht. Ursächlich für diese Korrelation könnte möglicherweise eine weibliche Vorliebe für philopatrische Männchen, welche den lokalen Dialekt benutzen, sein.

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