

# Introduce yourself at the beginning – possible identification function of the initial part of the song in the Great Reed Warbler *Acrocephalus arundinaceus*

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We analyzed a set of frequency and temporal characteristics of the introductory syllables in the song of the Great Reed Warbler (*Acrocephalus arundinaceus*) to assess their potential for individual recognition. We also tested if the initial syllables maintained their individual characteristics over a longer period by comparing their characteristics within a breeding season and over years for individually marked males. We found that within-male seasonal differences in introductory syllables were smaller than differences between males, which enabled correct classification of the majority of individuals within a season. However, the parameters of the introductory syllables of particular males tended to change over years, which diminishes the chances for correctly classifying males across seasons. Our results suggest that the introductory syllables of the Great Reed Warbler song contain sufficient information for male identification, but only within a particular season. As the studied syllables are found in nearly all songs of the Great Reed Warbler, including both long songs attracting females and short songs used during aggressive encounters with rival males or after pair formation, they may play an important function in both mate and rival recognition.



## 1. Introduction

The ability to discriminate or recognize conspecific individuals (IR = individual recognition) has been demonstrated for many songbird species (Beecher 1982, Lambrechts & Dhondt 1995, Johnstone 1997). Playback experiments have shown that responses to songs or calls of familiar

birds (neighbors, mates, parents or offspring) differ from responses to songs of unfamiliar individuals (Wiley *et al.* 1991, Molles & Vehrencamp 2001, Jouventin & Aubin 2002). IR is an important mechanism involved in social interactions and plays a crucial role in mate choice (Falls 1982, Wiley *et al.* 1991, Lind *et al.* 1996, Aubin *et al.* 2000, Charrier *et al.* 2001), neighbor recognition

(Stoddard *et al.* 1990, 1991, Godard 1991, Stoddard 1996, Molles & Vehrencamp 2001, Hyman 2005, Mackin 2005), territoriality (Falls & Brooks 1975, Aubin *et al.* 2004), parent-offspring communication (Falls 1982, Beecher 1988, Charrier *et al.* 2001, Lengagne *et al.* 2001), dominance hierarchies (Cucco & Malacarne 1999, Christie *et al.* 2004) and inbreeding avoidance (Sherman *et al.* 1997). Thus, from the receivers' perspective, a proper IR facilitates beneficial relationships and reduces costly aggressive encounters (Stoddard 1996, Stoddard *et al.* 1990, Molles & Vehrencamp 2001). On the other hand, as presented recently in an elegant review by Tibbetts & Dale (2007), there is a benefit to the signaler to be accurately recognized; hence selection acts on both parts of the signaler-receiver system. Therefore, we should expect better survival and higher reproductive success of those individuals who are better in recognizing others individually as well as those who have an individually recognizable signal.

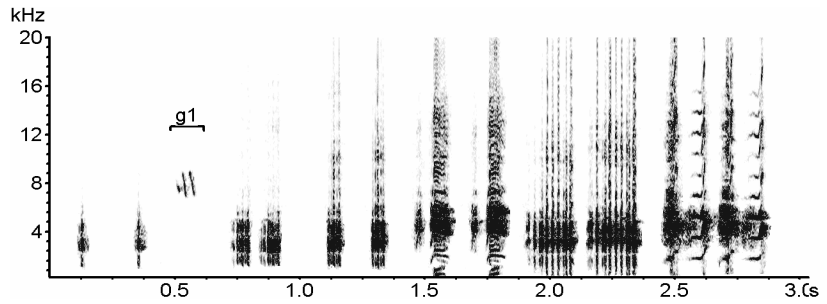
Although individual discrimination or recognition has been shown for over one hundred territorial bird species, the mechanisms of this process differ between species and are not yet fully understood (Tibbetts & Dale 2007). There are several reasons for that. For example, bird song is a multiple signal, which may carry several different messages at a time. Regardless of the signaler identity, the song may contain information about the individual quality, status, current needs or motivations (Gil & Gahr 2002). Therefore, an important question is where and how, within a song, the identity of an individual is encoded. Moreover, regardless of IR, song should be first assigned to the proper category of the species and/or local dialect (Nelson & Poesel 2007). Coding different kinds of information require different levels of character variability. For example, individual cues should be stable within and variable between individuals, while species cues should be sufficiently constant among all individuals within a species. Therefore, one may expect that different parts of a song or different song components (e.g., frequency modulation, amplitude modulation, note frequency and between-notes intervals) should be responsible for different messages. Some song characters may be redundant, as this may enhance recognition or perceptibility of other information in a noisy environment (Lengagne *et al.* 1999).

Until now, several specific features of song have been found to facilitate vocal IR in different species. For example, IR in some species is supported by the use of individually specific syllables or song type repertoires (Gentner *et al.* 2000, Griebmann & Naguib 2002). In species with high song-type sharing among individuals, different individuals may produce the same syllables (and consequently song types) in a distinctive manner using different frequency-temporal characteristics (Osiejuk *et al.* 2005). Sharing repertoires may not impede IR if individual repertoires contain distinctive combinations of shared song types or distinctive sequences in delivery (Gentner & Hulse 1998). Finally, general voice characteristics may be distinctive irrespective of song or syllable type (Molles & Vehrencamp 2001, Gilbert *et al.* 1994). Any song feature employed in IR should be characterized by low intra-individual variation and high inter-individual variation, and such variability should remain stable in time (Falls 1982, Stoddard 1996).

In the present paper, we present data on individually distinctive syllables within song of the Great Reed Warbler *Acrocephalus arundinaceus* (GRW) males. The GRW is a territorial songbird in which aggressive behavior is lower between established neighbors than between territorial owners and newcomers. Agonistic interactions are expressed the most by shortening the song, approaching and chasing the rival male away. If the opponent persists in singing both individuals are often involved in aggressive physical encounters (Węgrzyn 2006, the authors' pers. obs.). Neighbors mostly do not show agonistic behavior toward each other unless one of them enters the territory of the other. However, vocalization of a stranger (singing bird or a playback) elicits a strong aggressive response from all the nearby territory owners, even though the song comes from outside of their territories. We found this behavior useful in mist-netting and ringing males: the song of a stranger was played from a speaker adjacent to a mist-net, which attracted nearby males and allowed us set the mist-nets outside of the reed belts and territories of the males. This observation supports the view that GRW males are able to discriminate at least neighbors and strangers.

We analyzed a set of frequency and temporal characteristics of the introductory syllables in the

Fig. 1. An example of a Great Reed Warbler song. The introductory syllable g1 is shown as “g1” where most of the recorded Great Reed Warbler songs had that feature, irrespective of the further composition of the song.



song of GRW to assess their potential for individual discrimination. We selected one of the introductory syllables (g1, based on terminology used in Węgrzyn 2006) because it fulfills a number of criteria characteristic for a vocal signature. First, it is present in the majority of GRW songs, which cannot be said for any other syllable in the GRW repertoire. The high redundancy of this element predisposes it as a vocal signature, as most songs begin with g1 irrespective of their further composition (Fig. 1). Second, GRW males tend to shorten their song both in aggressive encounters and after pair formation to only few introductory

elements (Catchpole 1983). Location of g1 at the beginning of the song together with its consistent presence in a song structure further increases the probability of its functioning as an identity marker. Third, contrary to the other GRW syllables g1 are quiet close-range signals, audible from 2–4 meters only by human ear. This nature distinguishes them from advertising elements of the song, which in GRW can be audible from up to 1 km (Catchpole *et al.* 1985). In some species the element coding identity is also placed at the beginning of the song, and it is often a close-range sound that degrades over a distance (Aubin *et al.* 2004). Fourth, g1 is a type of whistle of narrow frequency band modulated in time with a number of frequency minima and maxima, which allows high variability and a consequent chance for coding identity of many individuals (Fig. 2). Fifth, preliminary visual analyses of g1 syllables derived from songs of different males demonstrate high inter-individual variation within the studied frequency parameters and relatively low intra-individual variation (Fig. 3).

In our study we tested if the g1 syllables maintained their individual characteristics both within a season and over a longer period. We compared characteristics of g1 of individually marked males from two observation sessions within a single season as well as from recordings over three consecutive years.

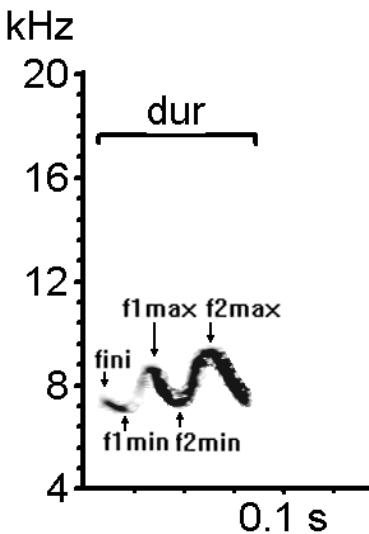


Fig. 2. Parameters of the introductory syllable g1 in the Great Reed Warbler song measured for analysis of vocal distinctiveness of individuals. 1 = initial frequency (*fini*), 2 = frequency of the first maximum (*f1max*), 3 = frequency of the second maximum (*f2max*), 4 = frequency of the first minimum (*f1min*), 5 = frequency of the second minimum (*f2min*), 6 = total duration of the syllable (*dur*).

## 2. Material and methods

### 2.1. Study area and specimens

The study was conducted during 2003–2005, from the end of April to the beginning of August. The 35-ha study area consists of 10 fish ponds in Korniaktów Północny near Rzeszów, south-east

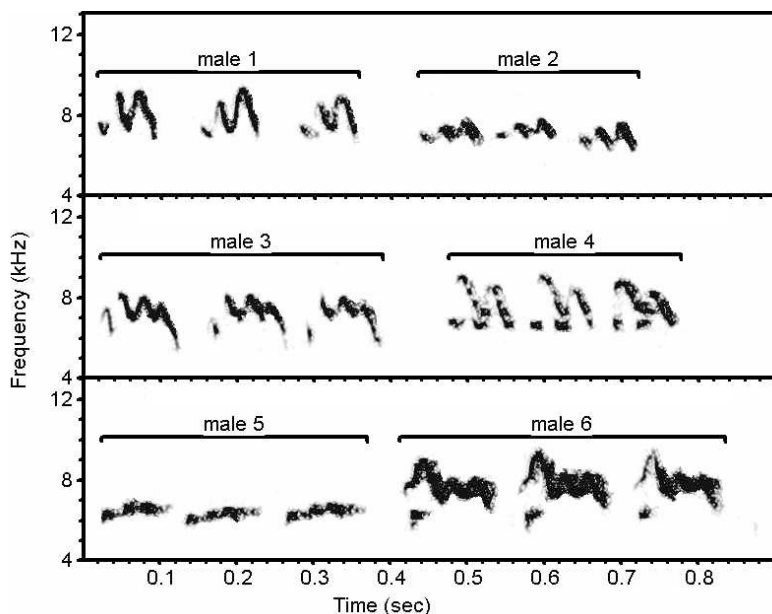


Fig.3. Visual presentation of inter-individual variation of introductory syllables g1 derived from songs of six different males.

of Poland (50°07'20" N, 22°22'23" E). The habitat of GRW consisted of more or less patchy reed beds growing along the pond banks with occasional shrubs and bushes. Each year 20–25 males were present within the ca. 35-ha study area. The majority of these males were banded and recorded. In the present study we used the recordings of only 12–16 males per season because the analyses of the g1 syllable required extremely high recording quality that was not always available. All recorded GRW males were mist-netted and individually color-banded. The recordings used in this study are a part of the data collected in a project concerning individual variation in the long song and song function in the GRW (Węgrzyn 2006).

## 2.2. Recordings and bioacoustics terminology

We analyzed the acoustic characteristics of the introductory g1 syllable for 12 males in 2003, 12 males in 2004 and 16 males in 2005. Three males were recorded in all three seasons, eight males were recorded in two seasons, and the remaining 15 males were recorded only in a single season. Altogether 26 males and 790 syllables were recorded. In a given season each male was continuously recorded for at least 10 minutes during a single session and most were recorded for 30 minutes.

The studied males were recorded from the distance of 2–4 m in two sessions. All recordings were made using a shot-gun microphone AKG C568 EB and Sony MZR 50 Mini Disc recorder. Sonograms were analyzed using Avisoft SASLab Pro 4.× software.

For each recording session of a given male we chose 18–25 g1 syllables of the quality that enabled measuring six parameters using sonogram screen cursor: initial frequency (*f<sub>ini</sub>*), two maxima (*f<sub>max1</sub>*, *f<sub>max2</sub>*), two minima (*f<sub>min1</sub>*, *f<sub>min2</sub>*) and the total duration of a syllable (*dur*) (Fig. 2). The choice of above parameters was due to initial analyses that indicated their relative individual stability.

In order to test if introductory g1 syllables remained unchanged in frequency and temporal parameters during a given season, we selected 11 males for which we had high-quality multiple recordings during a single breeding season recorded on separate days. The mean time between the two sessions of the same individual was 20 days (min = 5, max = 42, SD = 10.91). Whenever possible we chose the set of the temporally most distant recordings for each individual, and the time between sessions was longer than 2 weeks for eight birds. We used the above-listed parameters of introductory syllables as described above in further tests (see below).

### 2.3. Statistical analysis

To illustrate the potential for IR, we calculated the grand mean and standard error for all features of g1 syllables for all males separately for each study year. We also determined the between-male coefficients of variation ( $CV = [SD/mean]/100$ ) and the average within-male coefficients of variation based on the values from the g1 syllables for each male. We used the ratios of between-male to within-male coefficients of variation ( $CV_{bm}/CV_{wm}$ ) as a measure of relative between-male variability for each g1 feature (Table 1). The  $CV_{bm}/CV_{wm}$  ratio  $>1$  suggests that syllable feature is more variable between than within males and could be potentially used as a cue for IR (Bee *et al.* 2001). In an analogous manner we calculated ratios of between-years to within-year variability ( $CV_{by}/CV_{wy}$ ) for eleven males recorded in more than one season. The comparison of calculated ratios enabled direct comparisons of within- and between-male and between-year variability in g1 syllable parameters.

We used SPSS 12 PL software for performing statistical tests. Data are presented as means  $\pm$  SE unless indicated otherwise.  $P$  values are two-tailed unless stated otherwise. We used general linear models with repeated measures (GLM) to test if g1 syllable acoustic features differed significantly between recordings done at different sessions during a single season. We used ANOVAs (with Bonferroni probability adjustments) to test if there are significant differences in the studied syllable parameters within and between individuals in particular years or between years for particular males. We used discriminant analysis (DFA) to determine whether g1 syllables could be assigned to the correct male. In the DFA we applied the cross-validated classification and a leave-out-one test.

## 3. Results

### 3.1. Within-male syllable variation within a single season

We tested if g1 syllable features differed significantly between different recording sessions in a single season using repeated-measures GLM. Six syllable parameters showed significant differences between males recorded (Wilks' Lambda =

0.001,  $P < 0.001$ ), but the differences between recordings of the same male were non-significant (Wilks' Lambda = 0.962,  $P = 0.327$ ). Also the interaction between male and recording session was non-significant (Wilks' Lambda = 0.729,  $P = 0.314$ ). A test of between-subjects effects revealed that differences between recordings of the same males for the g1 syllable features were non-significant with probabilities between 0.147 and 0.491. A further discriminate analysis revealed that 94.1% of cross-validated cases were correctly classified to particular males regardless of the time when the recording was done. Thus, apparently the g1 introductory syllables remained unchanged during a single breeding season.

### 3.2. Differences between males

The  $CV_{bm}/CV_{wm}$  ratios indicated that all six g1 syllable features of the GRW songs were relatively more variable between males than within males, and this pattern was consistent in all three study years (Table 1). The ANOVAs demonstrated that this relationship of within-male and between-male variability was significant for every syllable feature tested. Consequently, the g1 syllable has the potential for providing recognition cues to the identity of the singing males. Subsequent discriminant analyses (DFA) showed that the accuracy of distinguishing between individuals based on the selected six features of g1 syllables is quite high. The cross-validated procedure allowed for correct assignment of syllables to individual males in 88% of the cases in 2003, 84% in 2004 and 92% in 2005. These values are well above random assignments, which were 8.3%, 8.3% 6.25%, respectively.

### 3.3. Within-male seasonal differences

Eleven males were recorded in two ( $n = 8$ ) or three ( $n = 3$ ) seasons. We used recordings of these males to test the relative between-season stability of the g1 syllable parameters. The values of the  $CV_{by}/CV_{wy}$  ratios for these parameters were significantly lower than those obtained for the  $CV_{bm}/CV_{wm}$  but still over the value 1 (Wilcoxon signed rank test;  $Z = -2.207$ ,  $P = 0.027$ ; Fig. 2). Subsequent tests revealed an ambiguous pattern of between-season

Table 1. Characteristics of the g1 syllable features with measures describing their within- and between-male variability, and ANOVA test for the between-male differences.  $CV_{wm}$  = within-male coefficient of variation,  $CV_{bm}$  = between-male coefficient of variation, and Max. between-male diff. (%) = maximum difference between individual means as a percentage of the grand mean.  $F$  ratios (single-factor ANOVA for log transformed values to meet normality assumption) compare the variability of a given syllable feature within and between males, with the degrees of freedom as follows: 11, 228 (2003), 11, 219 (2004) and 15, 303 (2005, except for the variable f2max with 15, 302).

Feature	Mean±SE	Range	Max. between-male diff. (%)	Avg. within-male CV (%)	$CV_{bm}/CV_{wm}$	$F$ ratio
2003, $n = 12$ males (240 calls)						
fini (kHz)	6.30±0.042	4.74–8.18	31.8	4.15	2.79	90.11*
f1max (kHz)	6.85±0.032	6.03–9.22	26.1	3.07	2.76	71.19*
f2max (kHz)	7.11±0.019	6.55–8.01	9.1	2.85	1.76	19.92*
f1min (kHz)	5.40±0.029	3.96–6.46	23.8	4.91	2.01	33.58*
f2min (kHz)	5.27±0.033	2.32–6.20	25.4	6.72	1.80	13.16*
dur (ms)	107.9±0.977	84–108	38.9	7.30	2.11	54.47*
2004, $n = 12$ males (231 calls)						
fini (kHz)	6.33±0.039	4.74–7.84	26.6	4.15	2.35	74.26*
f1max (kHz)	7.41±0.035	6.29–9.30	24.1	2.60	1.89	120.67*
f2max (kHz) <sup>a</sup>	7.35±0.026	6.63–8.70	17.0	2.32	1.76	72.85*
f1min (kHz)	5.57±0.030	4.39–6.55	24.1	3.60	2.58	91.42*
f2min (kHz)	5.45±0.031	4.22–6.98	26.5	4.74	1.65	45.77*
dur (ms)	106.2±1.201	62–146	58.6	7.13	2.58	97.36*
2005, $n = 16$ males (318 calls)						
fini (kHz)	6.10±0.030	5.18–6.97	29.3	3.60	3.03	90.71*
f1max (kHz)	7.29±0.033	5.89–8.01	28.9	2.75	3.49	139.55*
f2max (kHz)	7.27±0.028	6.12–8.04	25.4	2.58	2.93	121.53*
f1min (kHz)	5.57±0.025	5.13–6.67	27.6	3.58	2.97	56.51*
f2min (kHz)	5.62±0.025	5.05–6.56	26.7	4.15	2.13	46.66*
dur (ms)	97.3±0.783	69–117	49.1	6.74	2.35	74.20*

$CV_{bm}/CV_{wm}$  ratio >1 indicates that a given syllable feature was more variable between than within males; \* = Significant at  $P < 0.001$  after Bonferroni adjustment. a = for f2max in 2004, only 217 measurements fulfilled the recording-quality criteria and were included in the analysis.

Table 2. Evaluation of differences between years using a single-factor ANOVA for each syllable feature (see text for details). Bonferroni-adjusted  $P$  values are shown: \* = < 0.05, \*\* = < 0.01, \*\*\* = < 0.001, ns = > 0.05. a = Recorded in all three seasons.

Feature	Male nr.										
	1 <sup>a</sup>	2 <sup>a</sup>	3 <sup>a</sup>	4	5	6	7	8	9	10	11
<i>fini</i>	***	***	***	ns	*	***	***	***	ns	***	***
<i>f1max</i>	***	***	***	**	***	ns	***	ns	ns	***	***
<i>f2max</i>	***	***	***	**	ns	ns	ns	ns	*	***	***
<i>f1min</i>	***	***	***	ns	ns	**	***	***	***	ns	ns
<i>f2min</i>	***	***	***	ns	ns	ns	***	*	*	ns	ns
<i>dur</i>	ns	***	***	ns	ns	**	ns	***	***	ns	**

differences: we found significant seasonal differences in all except one syllable parameters (Table 2). The exceptional parameter concerned the three males recorded in all three seasons. For the remaining eight males recorded in two seasons we found significant differences in ca. 30% of cases (Table 2). Discriminant analysis conducted on pooled 2003–05 data for only males recorded in at least two seasons revealed a substantial decrease in the accuracy of correctly assigning syllables to a particular male in the cross-validation procedure, which was 62.7%.

#### 4. Discussion

We showed that the analyzed parameters of the introductory syllables appeared temporally stable within a season and enabled a correct classification of the majority of the studied individuals. On the other hand, parameters of the g1 syllables of particular males tended to change over years but the within-male differences still remained smaller than differences between males (Fig. 4).

Between-male differences in the introductory g1 syllable apparently contain sufficient information for identification of individuals. Correct classification of g1 syllables to individuals was between 88% and 92% every year. We not only demonstrated a significant diversity of g1 syllables between males but also their high stability over a season for a particular male.

The studied g1 syllables carry several features that caught our attention. The most obvious ones are that g1 is present in nearly all GRW songs and it is located at the same place in every song: at their very beginning. The described features of g1 hold not only for the population we studied but also for three other populations, recorded by us, in areas 500–700 km apart in Poland. Moreover, this quiet syllable is also visible on published sonograms of GRW vocalization from Germany (Catchpole 1983, Catchpole *et al.* 1986) and in commercial recordings (e.g., Roche 2003, Schultze & Dingler 2007). Due to its persistent presence in GRW songs irrespective of population, country, time and song type, g1 seems an important element of vocal communication in the GRW. It is also clearly different in amplitude, frequency and structure from the rest of the GRW syllables.

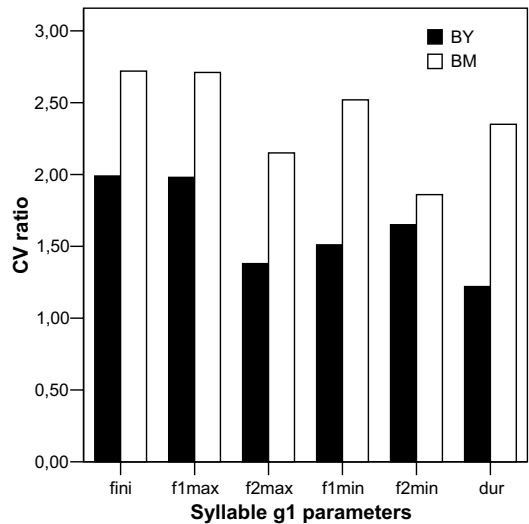


Fig. 4. Comparison of coefficient of variation ratios (CV) for Great Reed Warbler within-male differences in different seasons (■ BY) and between-male differences in the same season (□ BM). CV > 1 indicates a significant difference.

The number of frequency minima and maxima in the g1 syllable enables a high general variability and a nearly individual-specific coding identity. We showed here that GRW individuals make use of this characteristic by using personal frequencies and time intervals. Thus, g1 syllables may function as a vocal signature in the studied species. Although experimental evidence for IR function of g1 is lacking, we believe that the proposed functioning is more plausible than other possible functions of this syllable. As an element widespread within different populations with the same general structure and pattern, g1 may not be connected with dialects. Because of its limited audibility it does not serve as an advertising element of the GRW song but better functions as a close-range contact signal. While searching for vocal signatures it is very important to separate these from advertising elements, as otherwise the probability of differences in quality between individuals in distorting data becomes high (Dale *et al.* 2001).

We found a number of similarities between g1 syllables and vocal signatures used by other species. First, cues involved in IR are present in every song and located in the beginning (Elfström 1990), while those connected with species recognition are found in parts further along in the song (Aubin *et*

*al.* 2004). This sequence of features is explained by the fact that during territorial encounters there is a greater need of immediate individual recognition while the process of species recognition is accomplished already at a longer distance between signalers (Bradbury & Vehrencamp 1998). However, this is not a general rule as for different reasons IR cues might be organized in a manner that does not allow them to be located at any particular place within a song. For example, IR might be based on repertoire contents or voice characteristics (Lambrechts & Dhondt 1995). Second, many species perform specific quiet songs or songs that are built of parts characterized by substantially different amplitude and structure, which restricts their operating range (Dabelsteen *et al.* 1998). Selection on being recognized could depend on the distance between signaler and a potential receiver. For example, in the White-browed Warbler (*Basileuterus leucoblepharus*) a simple song consisting of several whistles is organized in such a way that the IR cues are characterized by relatively low amplitude and high overall frequency. As a consequence, they are most degraded in a tropical forest and “disappear” quickly during transmission, making birds anonymous at longer distances (Aubin *et al.* 2004). The g1 syllables, with their low amplitude, relatively high overall frequency and narrow frequency band width seem to be similar at least in propagation consequences. This similarity is remarkable because the reed belt is an acoustically hard environment with serious transmission difficulties (Heuwinkel 1982).

The evidence of individual differences in vocal parameters and the presence of other features characteristic for vocal signature do not prove that the cue would be used by the species for identification (Bard *et al.* 2002, Wiley 2005), as vocal differences have to be perceived by the receiver (Gentner 2000). Therefore, further experiments are needed to confirm if the differences in characteristics of the introductory syllable g1 play a role in identification of GRW individuals. This experimental approach is not easy, however, as identity cues may be coded also in other song features. As the GRW males perform song repertoires that are relatively stable within a season and do not share all their songs with neighbors (Węgrzyn 2006), one can expect this parameter to take part in identification as well. Of course, this fact does not di-

minish the possible function of g1 syllables in IR, as both cues – distinctive song repertoires and individually uttered introductory syllables – can complement each other in the identification process. Specific repertoires may be more useful for neighbor discrimination during the period of intensive singing, while the introductory g1 syllable can be of high importance in mate recognition after pair formation or during aggressive encounters (Catchpole 1983). As reported by Tibbetts & Dale (2007), a lot of information within a song can be coded in a redundant manner: thus, coding an individual’s identity in multiple cues seems plausible.

To avoid confusion with possible IR cues coded in distinctive songs or song repertoires, a proper experiment should be conducted on shortened versions of the song, characteristic for mate communication in GRW. We observed that the members of a pair mostly keep in close proximity to each other, probably due to mate guarding of a fertile female. However, sometimes they get separated, for example when scared away or during foraging. Following pair formation, the birds move low in the reed belts and at least occasionally cannot see each other. In such cases we observed that a male uttered a few introductory syllables and a female joined him after a while. One potentially good experiment to test IR functioning of the g1 syllable would be using a playback of introductory syllables of a familiar and strange male to a particular female. If the female would approach the speaker in response to the playback of the familiar but not that of the stranger, then the experiment would prove the IR function of the studied syllables. The difficulty of this approach arises from the fact that the observer may not always be able to see the female that usually moves low in vegetation. Recording the speaker approaches deep in the reeds may be possible by using reed vibrations as a cue, but more reliably by placing a mist-net around the speaker and a priori ringing the experimental females.

The remaining question is, why do the parameters of the introductory syllables change between seasons? This finding is not exceptional, as similar results have previously been obtained for frequency parameters of the voice of the Great Bittern (*Botaurus stellaris*; Gilbert *et al.* 2002). GRWs do not form pairs or neighbor groups that would last for more than one breeding season. Therefore a



vocal signature that remains constant over the years may not be of high importance for the focal species. Moreover, the quality and consequent breeding success of a GRW male generally increases with life span (Hasselquist 1998, Forstmeier *et al.* 2005). As a result, males may avoid linking their identity with their previous season quality.

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### **Esittelle itsesi esitapaamisella – rastaskerttusen laulun aloitusosan mahdollinen yksilöntunnistustoiminto**

Analysoimme useita laulun aloitusosan frekvenssi- ja aikamuuttujia rastaskerttusella (*Acrocephalus arundinaceus*) selvittääksemme aloitusosan mahdollista toimimista lintujen keskinäisessä yksilöllisessä tunnistuksessa. Testasimme myös, säilyttävätkö yksilöt aloitusosan tunnistettavat piirteet pidemmällä aikavälillä vertaamalla pesimäkausien sisäistä ja välistä vaihtelua yksilöllisesti merkatuilla koirilla. Havaitimme, että yksilön sisäinen vuosienvälinen vaihtelu aloitusosassa oli vähäisempää kuin yksilöiden välinen vaihtelu, minkä ansiosta valtaosa koiraista oli yksilöllisesti tunnistettavissa pesimäkauden aikana.

Aloitusosan parametrit kuitenkin muuttuivat vuosien välillä niin, että koiraiden yksilöllinen tunnistus vuosien välillä vaikeutui. Tuloksemme viittaavat siihen, että rastaskerttusen laulun aloitusosat sisältävät riittävästi informaatiota koiraiden yksilölliseen tunnistamiseen, mutta vain saman pesimäkauden sisällä. Koska tutkitut aloitusosat löytyvät lähes kaikista tallennetuista rastaskerttusen lauluista, sisältäen sekä pitkiä, naaraita houkuttelevia lauluja että lyhyitä lauluja käytettäväksi kilpailevien koiraiden kohtaamisissa ja pariutumisen jälkeisenä aikana, ne saattavat olla keskeisiä puolison ja kilpailijayksilön tunnistamisessa.

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