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Dialectal variation in the raincall of the Chaffinch *(Fringilla coelebs)*

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Several variations of the rülsch and huit Chaffinch raincall occur in mosaic fashion across the Bodanrück Peninsula in southwest Germany. In one area between huit and rülsch populations most birds produced hybrid hrreet calls. In four other areas rülsch and huit callers occurred syntopically along with a small number of hrreet callers. Data is presented indicating that huit and rülsch calls are cultural homologues.

Key words: Chaffinch, *Fringilla coelebs,* raincall dialects.

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Introduction

Although dialects in the raincall of the European Chaffinch *(Fringilla coelebs)* are well known in the early ornithological literature (review in Sokolowski 1965), most studies have been limited to onomatopoeic descriptions of these vocalizations (Sick 1939, 1950; Stresemann 1942). Spectrograms of a few call forms have been published (Marler 1956, Poulson 1958, Thielcke 1970, Knecht & Scheer 1968, Güttinger 1974) and recently two studies with more detail have appeared (Detert & Bergmann 1984, Bergmann et al. 1988). No quantitative study as yet exists, however, documenting variation within and between populations with different call types.

Variations in vocalizations are of great interest to students of evolutionary biology who have engaged in lively debate over their adaptive significance (Payne 1981, Baker & Cunningham 1985, Morton 1986, Rothstein & Fleischer 1987). Detailed studies on variation in avian vocalizations, in as many species as possible, are prerequisite to a meaningful evaluation of the adaptive significance of the phenomenon of dialects.

Chaffinch raincalls were recorded on the Bodanrück Peninsula, Lake Constance, southwest Germany (fig. 1) during the 1972 and 1973 breeding seasons in an effort to document the following: a) The number of distinguishable dialects in the study area. b) The amount and nature of individual, intrapopulational and interpopulational variation in each dialect region. c) The geographical limits of each dialect area. d) What occurs at the interphases or boundaries between two dialects: Are there sharp breaks between two call forms or are the changes clinal?

Data from the above permitted development of a schema on how new raincall dialects arise in continental Europe and on oceanic islands.

Methods and Materials

Raincalls were recorded in the field on Nagra III and Nagra IVL tape recorders using a Grampian dynamic microphone (type DP4) mounted on a twenty-four inch parabolic reflector unit. Tapes were analyzed on Kay Electric Sound Spectrogram machines (models 6062A and 7029A).

Some 3420 raincalls were recorded from 296 Chaffinches. With few exceptions, except for minor variations in duration and frequency from call to call each individual only used one raincall type. Only three individuals or 1.01% of the samples uttered two raincall types. Thus the first clean sound spectrogram from each individual was selected for quantitative analysis.

The following frequency (kHz) and time (seconds) measurements of various portions of the call were made directly from the spectrograms (fig. 2): 1. Highest frequency; 2. Lowest frequency; 3. Frequency spread; 4. Duration of the whistle portion; 5. Duration of the trill portion; 6. Total duration (4+5); 7. Ratio of the duration of the whistle to that of the trill (4/5).

The Study Area: A transect was made across the Bodanrück Peninsula in an area approximately 26 km × 6 km. Habitat types are treated in JACOBI et al. (1970) and consist mostly of Buchen *(Fagus)*, coniferous and mixed woodland separated by meadows or cultivated fields. Names of villages, towns, or hills are used as reference points for each dialect population herein described (fig. 1).

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Results

Three basic types of raincalls and their variants occured in the study area:

1. The Hui Raincall: This is the simplest form of the raincall, and consists of a whistle beginning at about 3 kHz, rising to about 5 kHz, with a frequency spread of about 2.55 kHz (fig. 3D). The duration of this call was about 0.11 s. This was the dominant call type on Mainau (fig. 1, area 11). Six of the eleven chaffinches recorded on Mainau used this call, and others were heard but not recorded. The other five birds used the "huit" form described below.

2. The Huit Raincall: In this form the upward inflected hui whistle is downslurred forming a vertical line on the spectrograph, and then upslurred again. The portion following the hui sounds like a click giving rise to the "it" portion of the huit (figs. 2A, 3C). The "hui" portion lasts about 0.075 s and the "it" portion about 0.03 s. This call was found in area 7 (fig. 1) which covered about 7 km × 5 km. Raincalls were sampled within a perimeter beginning from woods and orchards northwest of the village of Liggeringen. Southwest to Langenrain, south towards Allensbach, then northwest again to the woods near Markelfingen. This call was encountered again at Bodman (area 6). Areas 6 and 7 are probably contiguous, but time constraints and difficult terrain did not permit the author to sample areas in between.

3. The "Rülsch" Raincall: If the terminal ("it") portion of the huit is modulated rapidly up and down in frequency, at more than 40 times per s, a raincall ending in a rapid trill or vibrato results; this is the "rülsch" of THIELCKE (1970; fig. 2B, 3A and B). Four different variations of the rülsch raincall occur on the study area. These differ in total duration, and in the proportion of the whistle (hui) to trill (rülsch) portion of the call (table): (i) At Buchberg, coniferous woods south of Friedingen (fig. 1), an area covering about 1.5 km × 0.5 km, raincalls consisted of a short whistle of about 0.03 s followed by a trill of about 0.06 s. This is the shortest form of the rülsch on the Bodanrück, each raincall lasting about 0.08 s. (ii) Raincalls were sampled in woods covering 3 km × 1.5 km near Steisslingen (area 2). This is the longest form of the rülsch on the Bodanrück, averaging about 0.22 s (range 0.21 to 0.31 s). Each call began with a whistle portion of about 0.02 s followed by a trill of about 0.20 s. Sometimes the whistle portion was absent altogether (fig. 3 B). The trill portion was considerably longer than the whistle portion, with a whistle to trill ratio of 0.09. (iii) Raincalls

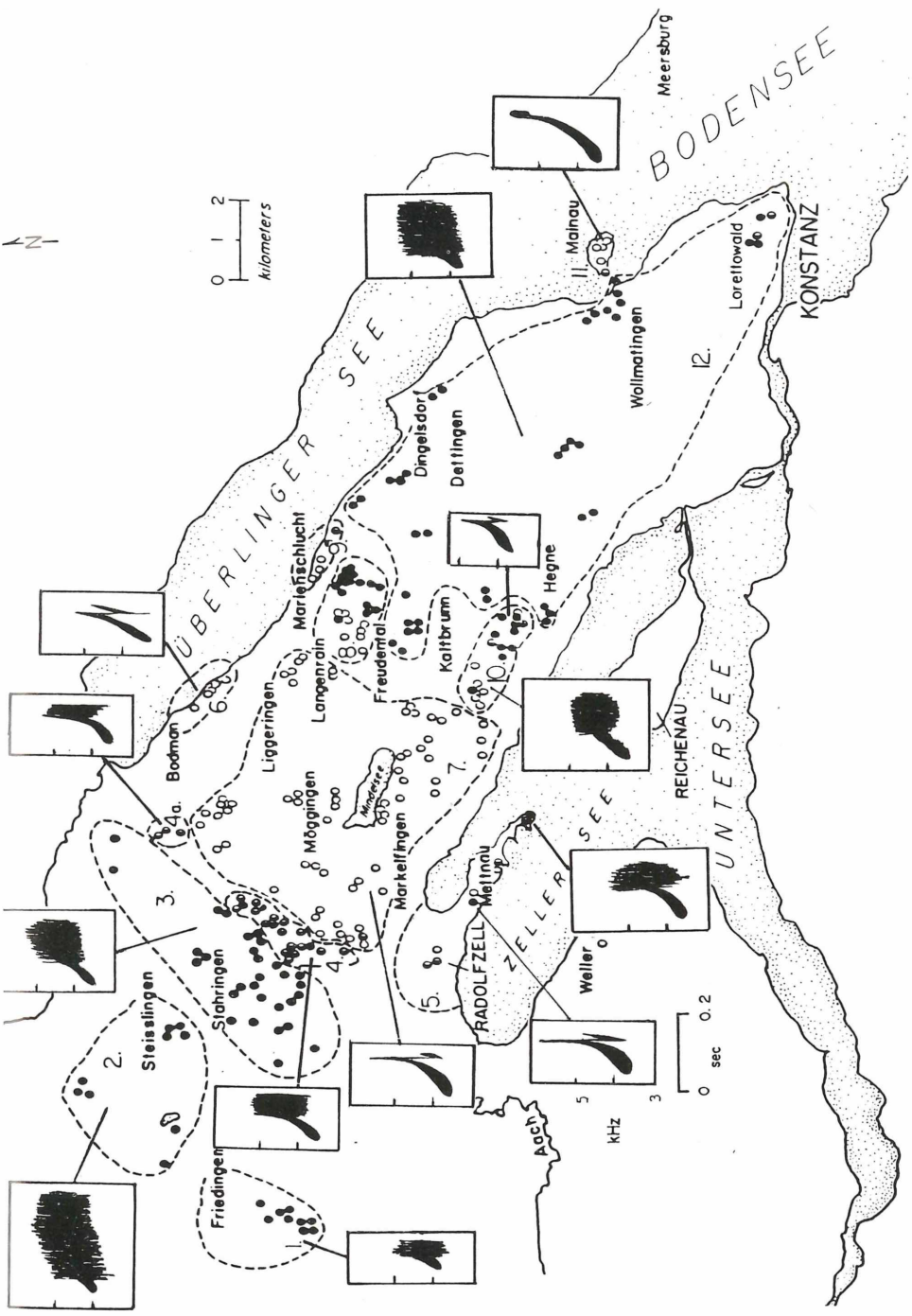

Fig. 1: Map of the study area showing sampling localities. Black symbols are areas where rülsch callers were recorded. White symbols are areas where huit callers were recorded and black-and-white symbols are areas with hybrid (hrreet) callers.

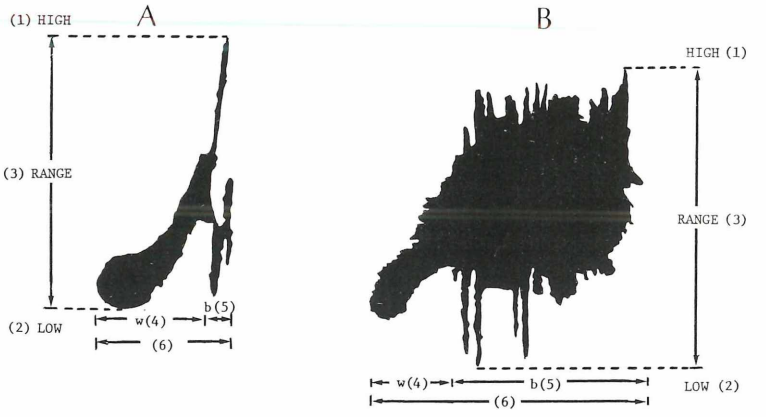

Fig. 2: A huit (A) and rülsch (B) raincall showing the six parameters measured (Table). 1. Highest frequency. 2. Lowest Frequency. 3. Frequency spread. 4. Duration of whistle portion. 5. Duration of trill portion (the "it" portion of the huit call in A is treated as a homologue of the vibrato in the rülsch call). 6. Total duration.

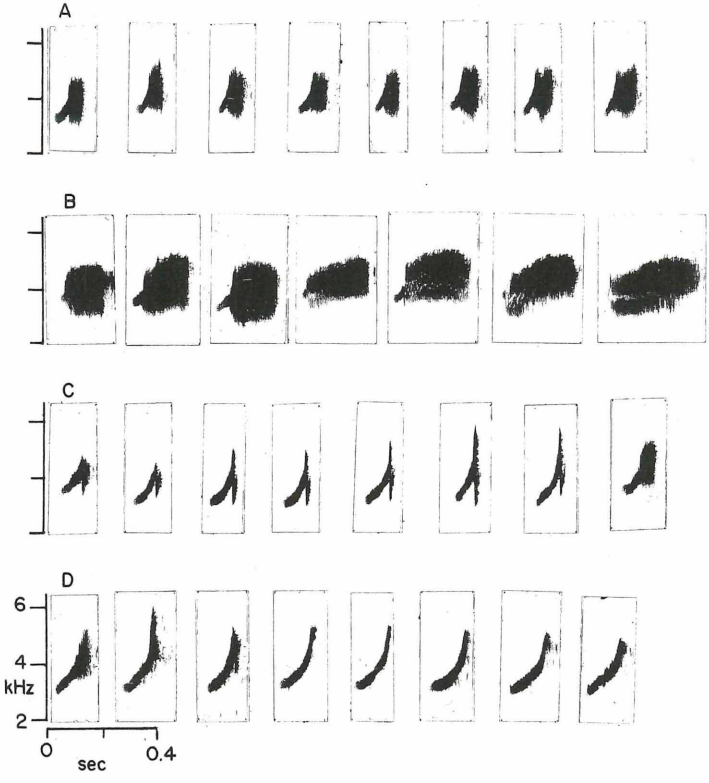

Fig. 3: Variation in raincalls in 4 sampled areas. A. Rülsch raincalls from eight chaffinches from Friedingen (area 1). B. Rülsch raincalls from seven individuals from Steisslingen (area 2). C. From left to right: seven huit and one rülsch raincall from area 7. This is the only rülsch recorded here. D. From left to right: three huit and five hui calls from Mainau.

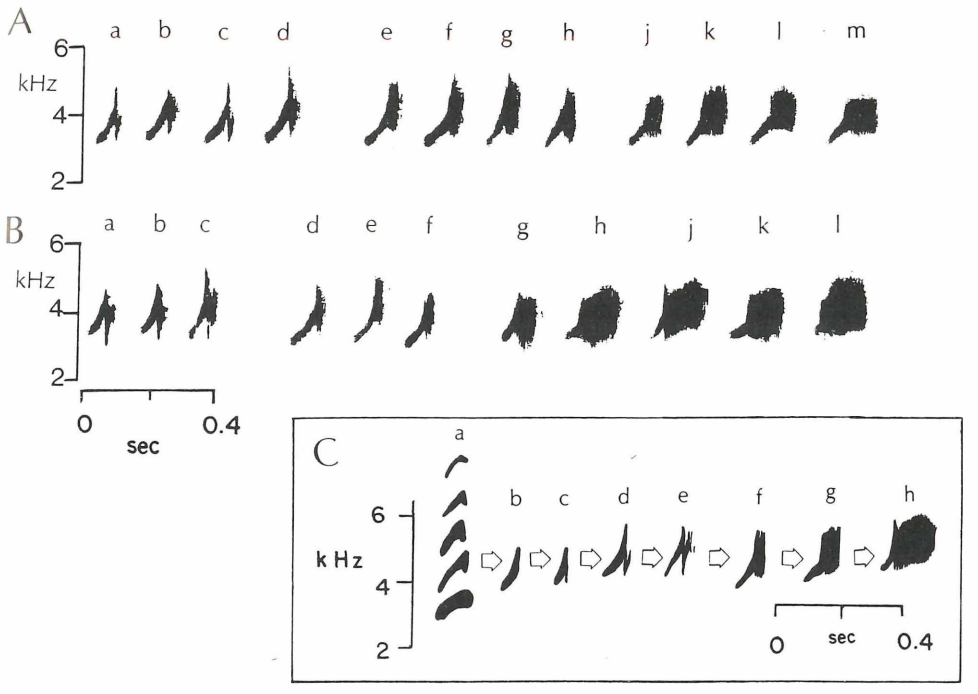

Fig. 4: A. Raincalls from the area 4 contact zone. From left to right: a to d are examples of huit calls, e to h are hrreet (hybrid) calls and j to m are rülsch calls. – B. Raincalls from the area 8 contact zone. From left to right: a to c are huit calls, d to f are hrreet (hybrid) calls, and g to l are rülsch calls. – C. [Insert] From left to right: Tracing of calls representing a graded series going from the "tew" juvenile call (a), to the hui (b) to the progessively more elaborate huit forms (c to e), to the hrreet form (f) to progressively more elaborate rülsch calls (g to h). Tracing of (a) from MARLER 1956.

were sampled in the woods near Stahringen and Stokach (area 3), an area covering about 8 km × 2 km. These calls were much shorter in duration than those in area 2, averaging about 0.16 s. Each call began with a whistle portion lasting about 0.04 s followed by a trill lasting about 0.12 s. (iv) Raincalls from area 12 included a transect from the village of Freudental to the city of Konstanz, an area covering about 16 km × 6 km. These raincalls were similar to those in area 3 but averaged slightly longer in duration (0.18 s).

Areas of contact between dialects

Five areas yielded birds using either huit or rülsch raincalls and/or cultural hybrids (hrreets) between the two. These are believed to be areas of secondary contact between previously separated subpopulations. 1. Most birds at area 4 (fig. 1) used raincalls that were intermediate in structure between those of the neighbouring huit and rülsch populations. This is especially noticeable in the durations of their trill portions which are 0.03 s in area 7 (huits), 0.12 s in area 3 (rülsch) and 0.06 s in the cultural hybrids, (fig. 4; table 1). To a lesser degree, introductory whistles were also intermediate in duration between the two parental populations: 0.04 s in area 3, 0.08 s in area 7 and 0.07 s in area 4. 2. East of Langenrain (area 8) a population of huit and rülsch callers occur syntopically (fig. 1). Mean duration of the trill portion is

Table: Descriptive statistics ($\bar{x} \pm sd$) of frequency and temporal parameters in Chaffinch raincalls (cf. Fig. 2).

AREA	N	High kHz	Low kHz	Freq.spread (kHz)	Dur. w. (s)	Dur. t. (s)	Total Dur. (s)	Ratio w/t	N recordings
1[1]	7	5.07±.17	3.25±.13	1.82±.17	.03±.005	.06±.01	.09±.008	.65±.20	37
			*	*	***	***	***		
2	18	5.17±.30	3.01±.21	2.125±.30	.02±.01	.20±.04	.215±.04	.09±.08	159
		***		***	***	***	***		
3	41	4.93±.21	3.07±.17	1.87±.20	.04±.02	.12±.02	.16±.02	.35±.16	371
				*	***	***	***		
4	49	5.03±.27	3.02±.17	2.01±.28	.07±.02	.06±.03	.13±.03	1.62±1.32	581
		**		**	**	***	***		
7	41	5.20±.35	2.99±.17	2.21±.37	.08±.02	.03±.01	.10±.02	3.83±1.97	543
				**	***	***	***		
12	35	5.06±.22	3.06±.18	1.99±.21	.05±.03	.13±.03	.18±.03	.44±.31	343
		**	*	***	***	***	***		
11	11	5.45±.40	2.91±.22	2.55±.33	.11±.02	.01±.02	.12±.01	8.45±4.95	171
4a	7	5.04±.25	2.82±.17	2.21±.31	.07±.01	.05±.01	.11±.02	1.39±.27	80
5	12	5.125±.28	3.125±.24	2.08±.24	.08±.01	.05±.02	.12±.02	2.11±1.14	155
6	4	5.0±.18	3.0±0	2.0±.18	.07±.0	.03±.01	.10±.01	2.33±.71	42
8	47	5.02±.22	3.18±.18	1.86±.28	.05±.02	.07±.04	.13±.03	1.30±1.11	522
9	9	4.94±.28	2.97±.18	1.97±.36	.07±.02	.05±.03	.12±.03	2.0±1.31	120
10	16	4.95±.31	3.08±.22	1.87±.27	.06±.01	.05±.02	.11±.02	1.60±1.00	296

[1] Adjacent populations listed above the line were compared, each numbered area compared to the area listed below, e. g. 1 vs. 2, 2 vs. 3 etc.; t – test significant levels are indicated by asterisks in between the specific values being compared: * = $p < .05$, ** = $p < .01$, *** $p < .001$. Areas 8, 9 and 10 were not included in the testing as they were contact zones with mixtures of raincalls from neighbouring populations. Areas 4a, 5 and 6 were not part of the transect and were also not utilized in testing.

0.07 s, which is intermediate between the 0.03 s of area 7 and the 0.13 s of area 12. However, few hrreet calls were recorded in this region. Visual inspection of the spectrograms revealed that 18 birds used huit calls, 25 birds used rülsch calls and 4 birds used hybrid calls. 3. Near Kaltbrunn (area 10) eight birds used the rülsch call, three used huits, and four used hrreets. 4. At Marienschlucht huit and hrreet callers occur. Again trill duration (0.05 s) is intermediate between those in area 6 (0.03 s) and area 12 (0.13 s). 5. Chaffinches residing in a small wood isolated at the tip of the Mettnau Peninsula used rülsch raincalls. These are separated by a marsh from birds to the north-west and in the city of Radolfzell which use huits and hybrid calls. One individuals used a rülsch call.

Descriptive statistics

There were significant differences in various frequency and temporal parameters between adjacent populations, each neighbouring pair differing in five to six of the characters measured (table 1). Mainau birds (area 11) used raincalls with a wider frequency range than those of mainland birds (fig. 3, table).

Discussion

Chaffinch raincalls on the Bodanrück may be classified as: (i) the huit or whistle form, (ii) the rülsch or vibrato form and the (iii) hrreet form which is hybrid between the two. (iv) On the Island of Mainau a variant (hui) of the huit call occurs which lacks the terminal click or "it" portion of the huit. Several forms of the rülsch call occur, each differing in total duration and duration of the whistle and trill portions (table 1).

DETERT & BERGMANN (1984) found that a large proportion of birds in a contact area uttered two call types. In contrast, few bilingual birds were encountered in this study (1.01%). Instead, four of the five areas situated between huit and rülsch populations contained birds using either call and few birds using hybrid (hrreet) calls. One area (area 4) yielded mostly birds using hybrid calls. This situation is analogous to that in song dialects of White-crowned Sparrows *(Zonotrichia leucophrys)*. In some contact areas two parental dialects and few "hybrid" songs occur (BAPTISTA 1975, TRAINER 1983), whereas other contact zones between two dialects yielded mostly birds singing hybrid songs (BAKER & THOMPSON 1985). Areas with two call types and few hybrid calls may represent populations that have only recently come in contact, whereas populations containing predominantly hybrid callers may represent older contact zones.

MARLER (1956) has described a harmonically rich "tew" call which is produced by juvenile Chaffinches and more rarely by adults (fig. 4). MARLER (1956; pers. obs.) has found intermediates between tew and huit calls and has argued convincingly that huits are derived from the juvenile call. The fact that various stages of intermediacy exist between the huit and the most elaborate form of the rülsch call of area 2 (Steisslingen) indicate that hui, huit and rülsch are cultural homologues (insert fig. 4).

Huit raincalls may develop in birds raised in isolation, whereas rülsch calls are apparently learned (POULSON 1951). However, song development studies in White-crowned Sparrows have yielded data indicating that vibrati may develop spontaneously from whistles (BAPTISTA, unpublished). It follows that rülsch raincalls in Chaffinches may probably develop spontaneously from huit calls of fledglings dispersing into isolated areas. These calls may be passed on by learning, improvised on and lengthened to produce the more elaborate Steisslingen form (fig. 3).

Conversely, improvisation may shorten the vibrato in a rülsch to produce a hrreet call (see Lorettowald, area 12) or to omit the vibrato altogether. Thus the same raincall types may be found in widely separated areas (THIELCKE 1970).

Vocal dialects probably develop as a result of geographic isolation, vocal tradition and the accumulation of cultural micromutations (BAPTISTA 1975). THIELCKE (1973) suggests that peculiar insular vocalizations may be a result of "withdrawal of learning" when juvenile founders arrive on islands before song learning is complete so that songs [or calls] develop as imperfect copies of mainland themes. The fact that Chaffinches countercall with raincalls (POULSON 1951; pers. obs.) suggests that male/male interaction is important in the proper development of raincalls. Juveniles dispersing into disjunct patches of habitat may develop novel raincalls if no adults are encountered to interact with and reinforce their learning. Thus patches of woods separated by meadows may yield distinct raincall dialects (THIELCKE 1970; this study). The hui call probably evolved on Mainau before the bridge with planted trees connected island to mainland, thus providing a dispersal corridor.

Zusammenfassung

Die „rülsch"- und „huit"-Regenrufe des Buchfinken variieren mosaikartig auf dem Bodanrück (Südwestdeutschland). In einem Gebiet zwischen „huit"- und „rülsch"-rufenden Populationen äußerten die

meisten Vögel den intermediären „hrreet"-Laut. In vier anderen Gebieten kamen „rülsch"- und „huit"-Rufer syntop mit einer geringeren Zahl an „hrreet"-Rufern vor. Die Befunde weisen darauf hin, daß „huit"- und „rülsch"-Rufe kulturelle Homologe darstellen.

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