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Comparative bioacoustics of territorial song in the Goldcrest *(Regulus regulus)* and its implications for the intrageneric phylogeny of the genus *Regulus* (Aves: Passeriformes: Regulidae)

With 17 Figures and 3 Tables

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Abstract. - The territorial songs of eastern Asian subspecies of the Goldcrest (*Regulus regulus*), - *tristis, japonensis* (Russian Far East and Japan), *himalayensis, sikkimensis* and *yunnanensis* -, are compared with one another and with those of the subspecies *regulus* and *teneriffae* and the species *R. satrapa* (N America). All the subspecies with disjunct ranges tend to have well-defined song regiolects; only the songs of *himalayensis, sikkimensis* and *yunnanensis* ("*himalayensis* complex") are acoustically uniform. The Goldcrest songs are all bipartite, consisting of a main and a final part. The main parts are constant within each subspecies, whereas each individual ♂ attaches variously modified final parts to the main part; this applies to all subspecies and to *R. satrapa*. An acoustic cline proceeds from the Himalayas through China (*himalayensis* complex), the Russian Far East and Japan to N America (*R. satrapa*). Along it, progressively more whistle elements ("C elements") are included in the verse, first forming a component of the final part (*himalayensis* complex) and then being integrated into the main part (*japonensis, R. satrapa*). The song forms in central Asia are the most primitive (*himalayensis* complex, *tristis*); forms derivative with respect to various characters are found in E Asia and the Nearctic (*R. satrapa*) as well as the W Palearctic (*regulus;* Canary Islands: *teneriffae;* Azores: *azoricus, inermis*). The response-eliciting parameters (tested by playback experiments in the field) are greatly reduced from one subspecies to another, as follows: in the nominate form as compared with *himalayensis, tristis, japonensis*/Russian Far East and /Hokkaido; in *japonensis*/Russian Far East as compared with /Hokkaido (song but not calls); in *japonensis*/Hokkaido as compared with /Russian Far East. Individuals of *sikkimensis* and *yunnanensis* respond vigorously to *himalayensis* song (Nepal). All acoustic characters give evidence of a complex evolution, at long temporal intervals, of *R. regulus*, in the course of which *R. satrapa* appears to have branched off. - Two hypotheses for the intrageneric evolution of *Regulus* are discussed. Both are based on the postulate that *R. calendula* is particularly old. One says that within the *R. ignicapillus*/*R. regulus* group the bipartite song (main and final parts) appeared first, the other that bipartite song was preceded by the eyestripe. In the first case the "eyestripe firecrests" (*R. ignicapillus, R. goodfellowi, R. satrapa*) are regarded as monophyletic and relatively recent, in the second as paraphyletic and early, with *R. regulus* as a later branch that constitutes a sister species of *R. satrapa*.

Kurzfassung. **Vergleichende Bioakustik des Reviergesangs des Wintergoldhähnchens *(Regulus regulus)* und seine Folgerungen für die Phylogenie der Gattung *Regulus* (Aves: Passeriformes: Regulidae).** - Die Reviergesänge ostasiatischer Subspezies des Win-

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tergoldhähnchens (*Regulus regulus*), - *tristis*, *japonensis* (Russisch-Fernost und Japan), *himalayensis*, *sikkimensis* und *yunnanensis* -, werden untereinander und mit den Subspezies *regulus* und *teneriffae* und mit *R. satrapa* (N-Amerika) verglichen. Alle disjunkt verbreiteten Subspezies neigen zu stark ausgeprägter Regiolekt-Bildung der Gesänge; nur *himalayensis*, *sikkimensis* und *yunnanensis* („*himalayensis*-Komplex") sind akustisch einheitlich. Alle Wintergoldhähnchen-Gesänge sind zweigeteilt in Haupt- und Schlußteil. Hauptteile sind innerhalb von Subspezies konstant; Schlußteile werden von jedem ♂ in unterschiedlicher Ausprägung an den Hauptteil angehängt; das gilt für alle Subspezies (und *R. satrapa*). Eine akustische Kline führt vom Himalaya über China (*himalayensis*-K.) nach Russisch-Fernost und Japan bis nach N-Amerika (*R. satrapa*). In deren Verlauf werden vermehrt Pfiff-Elemente („C- Elemente") in die Strophe eingefügt, zunächst als Bestandteil des Schlußteiles (*himalayensis*- K.), dann fest in den Hauptteil integriert (*japonensis*, *R. satrapa*). Besonders ursprüngliche Gesangsformen existieren in Zentralasien (*himalayensis*-K., *tristis*), nach unterschiedlichen Merkmalen abgeleitete in O-Asien und in der Nearktis (*R. satrapa*) sowie in der W-Paläarktis (*regulus*, *teneriffae*). Die reaktionsauslösenden Parameter (getestet in Rückspielversuchen im Freiland) sind zwischen einzelnen Subspezies stark reduziert, wie folgt: bei der Nominatform gegenüber *himalayensis*, *tristis*, *japonensis*/Sibirien und /Hokkaido, bei *japonensis*/Russisch-Fernost gegenüber /Hokkaido (Gesang und Rufe), bei *japonensis*/Hokkaido gegenüber /Russisch-Fernost und *himalayensis*. *Sikkimensis* und *yunnanensis* reagieren heftig auf *himalayensis*-Gesang (Nepal). Alle akustischen Merkmale untermauern eine komplexe und zeitlich stark gestaffelte Evolution von *R. regulus*, die *R. satrapa* einzuschließen scheint. - Zwei Hypothesen der intragenerischen Goldhähnchen-Evolution werden diskutiert. Beide gehen davon aus, daß *R. calendula* besonders alt ist. Innerhalb der *R. ignicapillus*/*R. regulus*-Gruppe entstand entweder zuerst ein zweigeteilter Gesang (Hauptteil/Schlußteil) oder der Augenstreif. Im ersten Fall gelten die „Augenstreifen-Goldhähnchen" (*R. ignicapillus, R. goodfellowi, R. satrapa*) als monophyletisch und spät entstanden, im zweiten Fall als paraphyletisch und *R. regulus* als Schwesterart zu *R. satrapa* als später Abzweig.

Introduction

Songbirds of the genus *Regulus* have always presented a challenge to systematists. There has been no agreement so far as to the number of species (five: Morony & al. 1975, six: Sibley & Monroe 1990, Glutz v. Blotzheim & Bauer 1991) and their taxonomic rank, nor as to the systematic position of the genus. However, there is a growing body of evidence that it should be considered a distinct family, the Regulidae (Morioka 1960, Sibley & Ahlquist 1990), separate from the Sylviidae (Vaurie 1959, Cramp 1992). As yet the status and relationships of widely disjunct forms also remain obscure, whether these are distributed in Eurasia and North America or limited to Atlantic and Pacific islands (Voous 1962, Sibley & Monroe 1990). The only interpretation likely to be well founded is that *Regulus* colonized the Nearctic from eastern Asia, possibly several times (Stepanyan 1966, Ingold & al. 1988, Löhrl & Thaler 1992). The question of the closest relatives of the Goldcrest (*Regulus regulus*) and the Firecrest (*R. ignicapillus*) in North America remains also controversial. A number of attempts have been made to establish species by assembling different forms in various ways (Hartert 1907, v. Boetticher 1941, Voous 1962, Desfayes 1965, Mayr & Short 1970, Becker 1978, Thaler 1990b, Sibley & Monroe 1990, Glutz v. Blotzheim & Bauer 1991, Cramp 1992, Eck 1996); none has been accepted without dispute.

In our present consideration of the systematic problems, we focus chiefly on the geographic variability of territorial songs. *R. regulus* is the most widespread member of the genus within the Palearctic (Fig. 1), with a pattern of distribution that represents all the phenomena known to be involved in the processes of speciation. Its range comprises large, nearly transpalearctic areas as well as small isolated populations on Atlantic islands, and in some cases the acoustic differences are considerable. Apart from the island populations, the greatest morphological diversity, as measured by the number of recognized subspecies, is found in Asia (Vaurie 1959, Glutz v. Blotzheim & Bauer 1991, Cramp 1992). We shall place the Asian populations in the foreground, but in addition include the Nearctic *R. satrapa*. We take as a point of departure the thorough studies by Becker (1974, 1976, 1977a, 1977b,

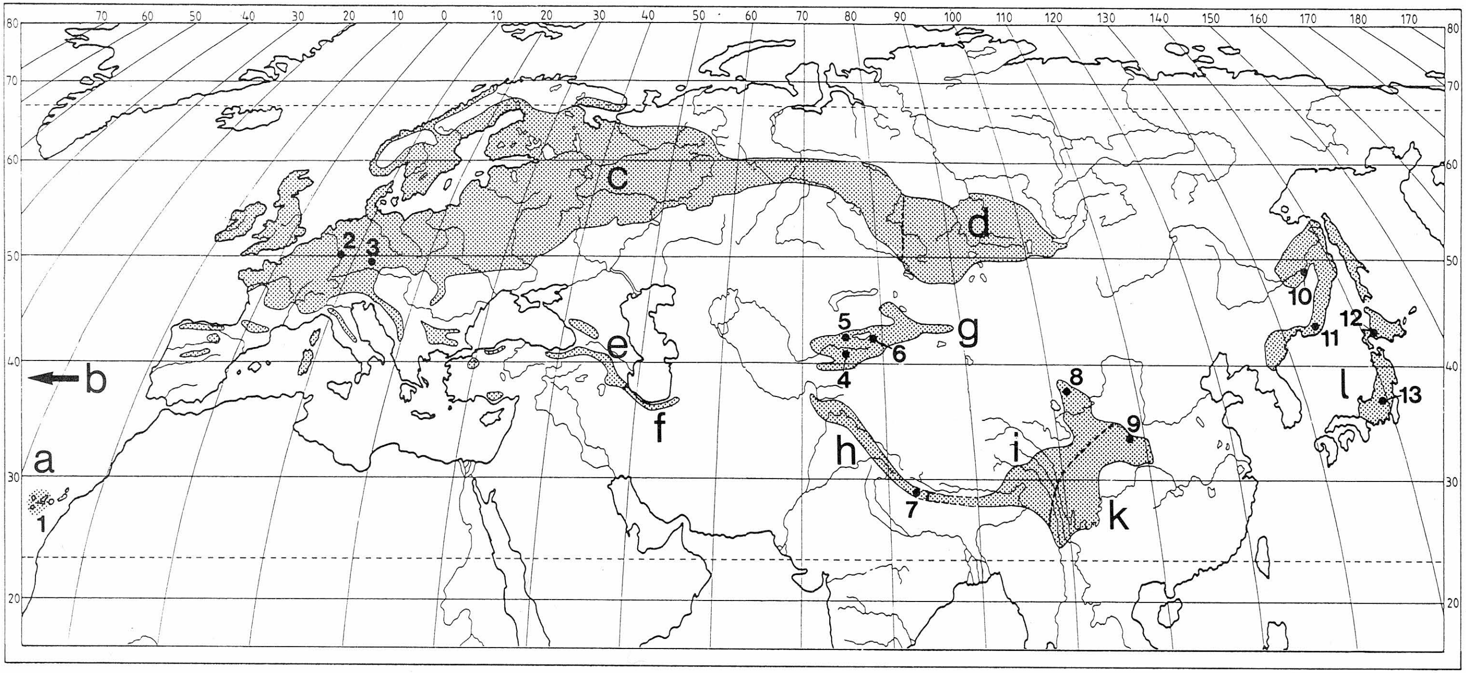

Fig. 1: Distributional area of the Goldcrest (*Regulus regulus*) indicating recognized subspecies. - a) *teneriffae*; b) *azoricus, inermis, sanctaemariae*; c) *regulus*; d) *coatsi*; e) *buturlini*; f) *hyrcanus*; g) *tristis*; h) *himalayensis*; i) *sikkimensis*; k) *yunnanensis*; l) *japonensis*. - Numbers indicate the locations where tape-recordings used in this study were made (see details in the respective subspecies sections). - 1) Tenerife, Canary Islands; 2) S Germany; 3) W Czech Republic; 4-6) Kirghizia (4: Sari-Tshelek, 5: Bishkek, 6: Przewalsk); 7) Nepal; 8) China, Qinghai Prov.; 9) China, Shaanxi Prov.; 10-11) *japonensis*, Russian Far East (10: S Chabarowsk, 11: S Sikhote Alin Mts.); 12) Japan, Hokkaido; 13) Japan, Honshu. - Drawn from various sources.

1978), Löhrl & Thaler (1980, 1992) and Thaler (1990a, 1990b) on the acoustic behaviour of western Palearctic Goldcrests.

Materials and Methods

Recording apparatus: Several models of the UHER series (Nepal 1973); Nagra SN (Russia 1990, Kirghizia 1993, Nepal 1995, China 1996, 1997); Sony Walkman WM-D6C (Russia 1996, Japan 1996). - Microphones: Sennheiser MD 211 N in combination with parabolic reflector 80 cm diameter (Nepal 1973), plastic reflector 60 cm diameter with microphone Telinga Pro III (Russia 1990, 1996, Kirghizia 1993, Nepal 1995, China 1996, 1997, Japan 1996). Loudspeaker for playback experiments: Sony SRS-38. Sonagraph: Kay Elemetrics DSP 5500; all figures show original sonagrams, filter width 300 Hz, screen time axis 2 s.

Procedure for playback experiments: Test and control songs were broadcast by a loudspeaker with 10-m cable. Playback of a foreign song type, always with repetition of the same song (10 times in succession, with 2-s pauses between the individual songs), 2-min pause following this series, then playback of a series of 10 songs of the population's own song type as a control. Test songs were chosen partly for dissimilarity, partly for similarity to the song types of the populations where the experiments were carried out.
The reactions of the tested individuals were divided into three groups. a) If the bird approached the loudspeaker to within a distance of 10 m and displayed at least minimal territorial behaviour (wing-flickering, display-flight, forward-display, calls, song), the reaction was classified "highly agressive", b) an approach to more than 10 m distance a "less agressive" reaction, c) no obvious approach "no reaction". To judge the responsiveness of C European Goldcrests in general a double test (conditions as described above) was carried out but with test and control song identical. All individuals (n = 14) reacted, most of them highly agressively, on both first and second playback. No habituation occurred within test pairs. The individual ♂ was tested only once with one test pair, but often with a different pair at least one week later.

Definitions of terms: Pulse: a component of a call distinguished by a frequency-modulation pattern. Pulse rate: number of repeated brief pulses per unit time. Element: uninterrupted sound event, which appears solid black in the sonagram; there are various types (see below). Element group: arbitrary combination of at least two types of elements, may be produced in series in main parts of a verse. Phrase: passage formed by repetition of any single element. Trill: passage formed by repetition of a single type of conspicuously short element in the main part of a verse. Trill rate: number of elements per unit time.
The following types of elements are distinguished: "A", short hook, open downwards, with narrow frequency band (Fig. 3a); "B", strongly frequency-modulated element, similar to a call (Fig. 5h); "C", whistle with steeply descending initial part (Figs. 3a, 4b); "D", whistle with no distinct initial part (Fig. 4b).
UPGMA = Unweighted pair-group algorithm with arithmetic means, resulting in a phenogram.

Experiments with recorded songs: Playback locations and songs tested. In SW Germany: in two populations (Kaiserslautern and Taunusstein/Taunus) 8 songs were tested on Goldcrests, 6 of which were also tested on Firecrests (*Regulus ignicapillus*); test songs recorded from: *himalayensis*/Nepal (Fig. 14, TS 1-3), *tristis*/Kirghizia (TS 4, 5), *japonensis*/Russian Far East (TS 6), *japonensis*/Hokkaido (TS 7,8). In Russian Far East: playback of one song and one call series recorded from the Hokkaido population (Fig. 15, TS 7, 8). In Hokkaido: playback of one song recorded from the *japonensis* population from Russian Far East (Fig. 15, TS 6) and one *himalayensis* verse from Nepal (Fig. 15, TS 1).

Results

Bipartite structure of the territorial song

All the Goldcrest populations so far investigated sing a compound verse comprising (a) a main part and (b) a final part (Becker 1974, 1978). The main part (a) begins somewhat differently in various major populations, with either a trill, in which a single element is repeated (e.g., *r. himalayensis*), or a series of element groups, each comprising 2-5 elements of different types (includes the „Anfangsteil" of *r. regulus* [= initial part in Becker 1974]).

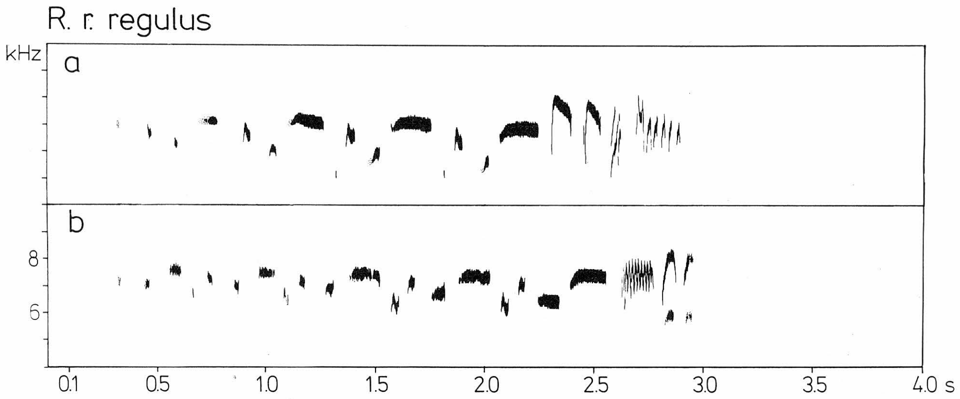

Fig. 2: Full territorial songs of *R. r. regulus*. - a) Taunusstein, SW Germany; b) Czech Republic, Šumava National Park.

This introduction is followed by a variable phrase. The phrase section, depending on the major population or subspecies, comprises either B or C elements (cf. Figs. 5h; 3a, 4b). In certain subspecies the initial section is sometimes omitted (in the case of *R. r. tristis* and in *R. satrapa*), in which case the variable phrase section is correspondingly prolonged. The final part (b) is less than half as long as the main part and consists of a sequence of very diverse elements within a broad frequency band, often broader than the range of frequencies represented by all elements in the main part. After the stereotyped, immutable main part each individual ♂ can add different final parts - a feature by which a listener can readily distinguish the main from the final part.

Regulus regulus regulus (Fig. 2)

Widest distribution of all subspecies, ranging from Spain to W Siberia (Fig. 1).

Material: Numerous recordings from various parts of Germany and the western Czech Republic (Šumava).

Auditory impression: Delicate, agitated whispering verse, becoming gradually louder and with an emphatic final part.
For vocalizations of the nominate form see BECKER (1974, 1977a), BERGMANN & HELB (1982), GLUTZ V. BLOTZHEIM & BAUER (1991), CRAMP (1992). Here we give only a brief sketch (Fig. 2).
Syntax: The verse comprises two parts, a main and final part (Fig. 2). At the beginning of the main part are 1-5 similar elements in about the same frequency range; this introductory part (see BECKER 1974) is followed by a regular sequence of element groups, each composed of 4-5 elements. These include only slightly modulated whistles of varying length as well as short A elements (hooks opening downward); there are pronounced frequency jumps between the elements. These element groups range in frequency between 4.8 and 8 kHz. The syntactic structure of the main part is extremely constant, with departures from the rule only in isolated marginal populations of SW Europe (BECKER 1977a).

Final parts: Whereas an individual ♂ always sings the same main part, including the introduction, each ♂ can produce many final parts, each of which is in itself constant. We have recorded as many as 12 (Taunusstein) or 15 (Czech Republic) final parts. BECKER (1974) found up to 18 for one ♂, and 41 different final parts in a narrowly circumscribed

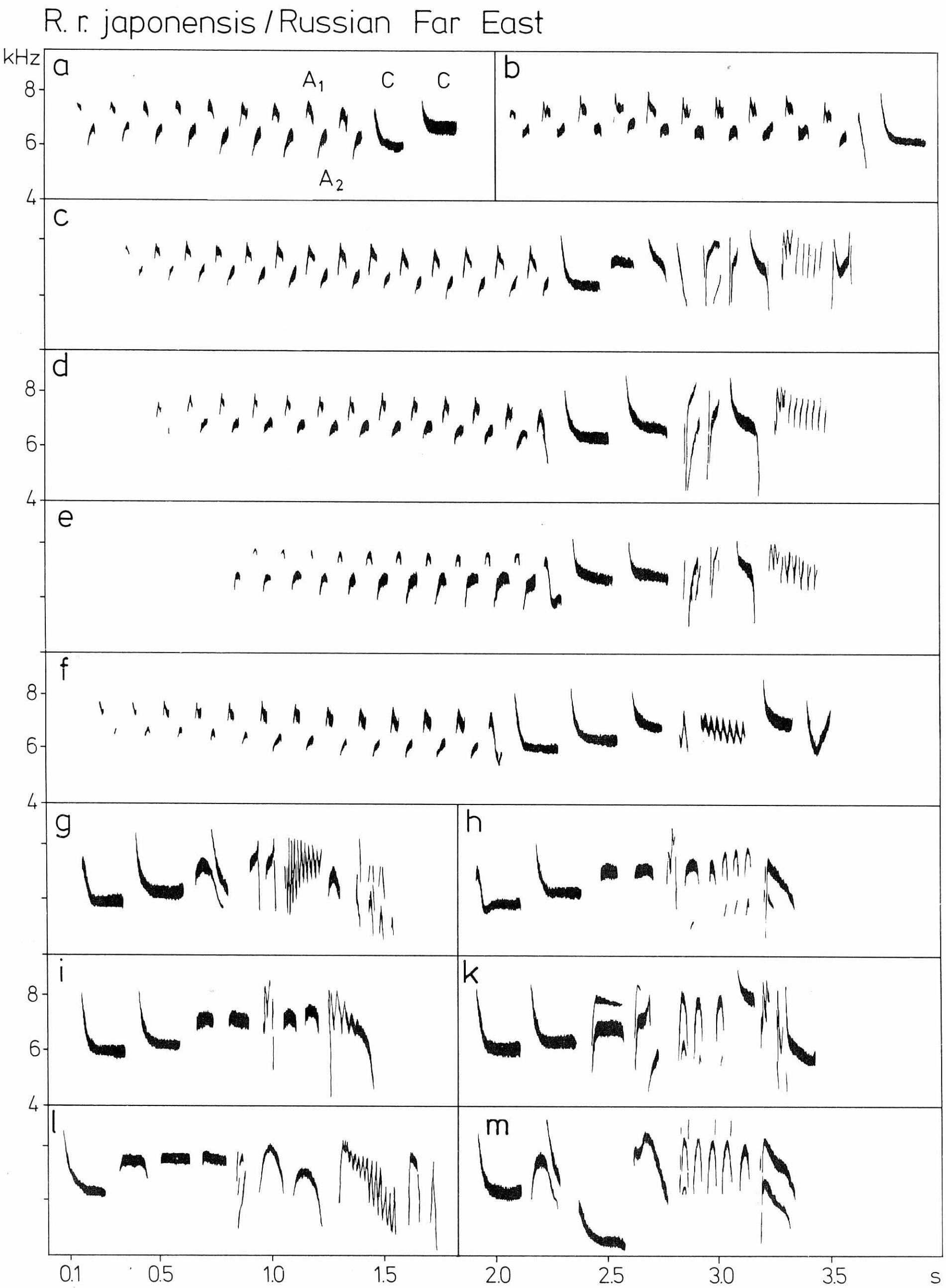

Fig. 3: Territorial song of *R. r. japonensis* in the Russian Far East. - a-f) full territorial songs, g-m) final parts of territorial song. - a, c, f-m) Chugurievka; - b, d) Oblatchnaya Mt.; - e) Chabarovsk. - c-e) song type with congruent final part from 3 populations; f-m) repertoire of 1 ♂ with differing final parts.

	Hokkaido	Russian Far East	
	element 1	element 1	element 2
shape	˺	^	^
maximal frequency (kHz)	7,9	7,8	6,9
minimal frequency (kHz)	5,1	7,0	6,3
frequency modulation (kHz)	2,8	0,8	0,6
frequency difference between E_1/E_2 (kHz)		0,93	
frequency bandwidth E_1/E_2 (kHz)	2,8	1,65	

C phrase (all values in kHz)

Hokkaido				Russian Far East			
	C_1	C_2	C_3		C_1	C_2	C_3
syntax 1	6,0 - 6,2	7,0 - 7,1		syntax 1	6,3 - 6,4	7,1 - 7,2	
syntax 2	6,2 - 6,4	6,5 - 6,8	6,6 - 7,0	syntax 2	6,2 - 6,4	6,8 - 7,0	6,9 - 7,2
syntax 3	5,6 - 5,9	5,6 - 5,9	6,4 - 6,5	syntax 3			

Tab. 1: *R. r. japonensis*, measurements of main parts.

population with 22 ♂♂, many of which had overlapping repertoires. Final parts are characterized by their variable syntax and broad frequency bands. Occasional imitations of other species are inserted only into the final parts.

Regulus regulus japonensis (Fig. 3)

Mainland populations in the Russian Far East and on Honshu.

Material: Far eastern Russia, Sikhote Alin Mts., upper reaches of Ussuri river, 30 km SW of Chugurievka, 7 ♂♂, M. P. 21.-25.5.1996; - Sikhote Alin Mts., 7 km S of summit of Mt. Oblatchnaya, 12 ♂♂, M. P. 26.-28.5.1996; - Bolshekhekhzira Reservation 25 km S of Khabarovsk, 1 ♂ 11 songs, J. M. 9.6.1990. - Honshu: central part, Nagano Prefecture, Mt. Nishihodaka (about 36°15' N, 137°40' E), T. Kabaya, July 1960, 1 ♂, 4 songs (KABAYA & MATSUDA 1996). - In total 279 songs, 21 ♂♂, 4 localities.

Auditory impression: Very uniform; the main part sounds like a trill (with a single type of element); final part set off from the rest, with clearly audible variations.

Syntax (Fig. 3): The main part consists of the multiple repetition of an element group comprising 2 A elements, after which follows a short phrase of whistles (C elements). The first structure, the series of element groups, is stereotyped and the same for all ♂♂. The first element of the group, A_1, is higher than A_2 (data in Table 1), so that there is a downward frequency jump in each group; the repetition rate is 6.2-7.7 element groups per s. The whistle phrase is also characterized by marked frequency jumps between consecutive C elements, so that it can be subdivided into two syntactic structures (data in Table 1). A single ♂ can perform several syntactic structures.
The three populations investigated are very similar with respect to the main part of the song, including the C elements, although two of the recording sites in Russia (S Khabarovsk and Oblatchnaya Mountain) are 1000 km apart. Even the final parts can be identical in widely separated populations (Fig. 3d and e).

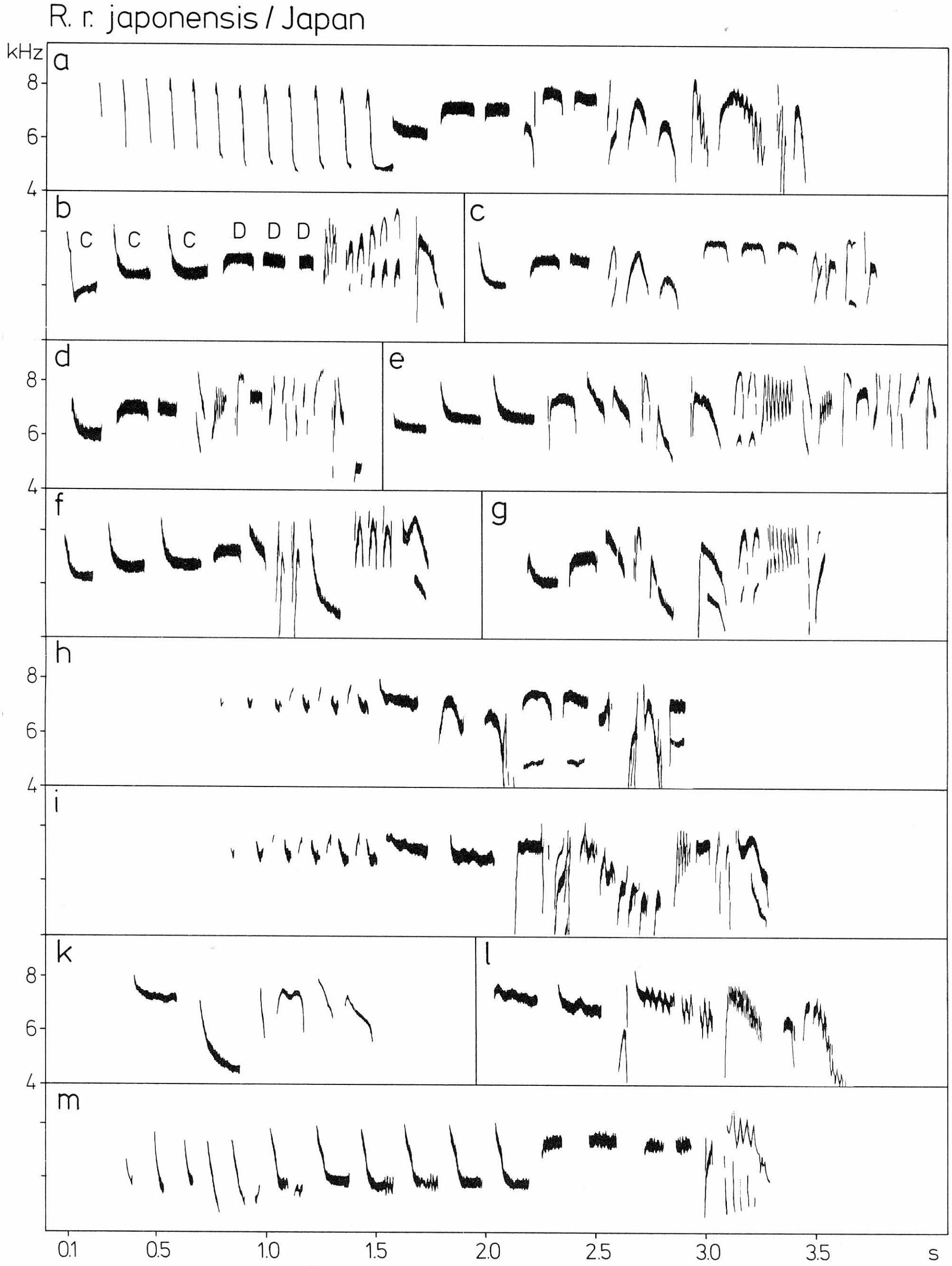

Fig. 4: Territorial song of *R. r. japonensis* in Hokkaido, Japan (a-g: Sapporo National Forest, m: not localized), and in Honshu (h-l: Mt. Nishihodaka). - a-g) 1 full song (a) and final part repertoire of 1 ♂ (b-g); - h-l) 2 full songs (h-i) and final part repertoire of 1 ♂ (k-l, including C elements).

Final parts: We found 38 variations altogether at the three widely spaced recording sites, of which 5 were sung by more than 50 % of the ♂♂, 19 by only one ♂; maximally 15 per ♂ (Fig. 3f-m).

On Honshu the *japonensis* territorial song has the same verse structure as on the Russian mainland (repetition of a 2-element group in the main part, Fig. 4h-l). The C phrase of this ♂ falls in pitch, unlike those of *japonensis* on the mainland and in Hokkaido (see below).

Regulus regulus japonensis (Fig. 4)

Insular populations in Hokkaido.

Material: Hokkaido: National Park of Sapporo City, 14 ♂♂, M. P. 14.-15., 18.-19., 24.6.1996; - Commercial CD, Shufunotomo Co., bird song 3, 1 ♂ without locality indication; - In total: 261 songs, 15 ♂♂, 2 loc., 1 unlocalized (from CD Shufunotomo Co.).

Auditory impression: The whistle series in mid-verse is longer, making the song more conspicuously tripartite than that of the Siberian population; the whistles are so loud as to dominate the verse.

Syntax (Fig. 4): The main part consists of a simple trill and a whistle phrase comprising 1-9 C elements. The trill is stereotyped and contains only extremely short, nearly click-like elements, at progressively lower frequencies that span a wide range (cf. Table 1). The individual element begins with a brief upstroke, the lower end being slightly drawn out to produce a club shape. The verse begins quietly, so that the initial elements are incompletely represented in the recording. The trill rate is 8.7 elements/s.
The whistle phrase (C elements) varies among individuals in its length and the size of its frequency jumps. The number of C elements is on average higher than in the mainland population, but the syntactic structures are similar (data in Table 1). A rare ♂ will produce whistles spanning the full frequency range of 5.7-7.2 kHz (Fig. 4m), but most sing only in parts of this range.
This syntax form (Fig. 4m) does not occur in the Russian Far East (cf. Table 1); it is characterized by a series of C elements at approximately the same low frequency that is terminated by one (or two) large increases in frequency (data in Table 1).

Final parts: We documented 40 variations, of which 6 were sung by more than 50 % of the ♂, 17 only by one ♂; a single ♂ was able to perform at most 22 variations.

Regulus regulus himalayensis, R. r. sikkimensis, R. r. yunnanensis ("*himalayensis* complex", Fig. 5)

Populations from Pakistan to central China (Fig. 1). These three continuously distributed subspecies are treated together here because their songs are so homogeneous that they can be considered a single entity.

Material: *himalayensis*: Nepal, E and N Dhaulagiri area in Mustang and Dolpo Distr., 83 songs, 4 ♂♂, 3 localities, J. M. 3.-4.6., 13.6.1973, 12.5.1995; - *sikkimensis*: China, Qinghai Prov., Bei Shan, Datong Valley, 98 songs, 2 ♂♂, 1 loc., J. M. 1996; - *yunnanensis*: China, Shaanxi Prov., Qinling Shan, Taibai Shan, 52 songs, 2 ♂♂, 1 loc., J. M. 13.-15.6.1997.

Auditory impression: The highest-pitched of all *regulus* songs.

Syntax: The main part consists of a trill comprising a single element repeated at an extremely high rate. The type of element differs even among subpopulations: simple downstrokes (Fig. 5c,g), hook opening upward (Fig. 5f) or downward (Fig. 5b,d). Average frequency maximum 8.6 kHz, minimum 6.9 kHz (^F = 1.7 kHz). Individuals can reach frequencies as high as 8.1 kHz (*sikkimensis*/*yunnanensis*) or 9.4 kHz (*himalayensis*). Trill

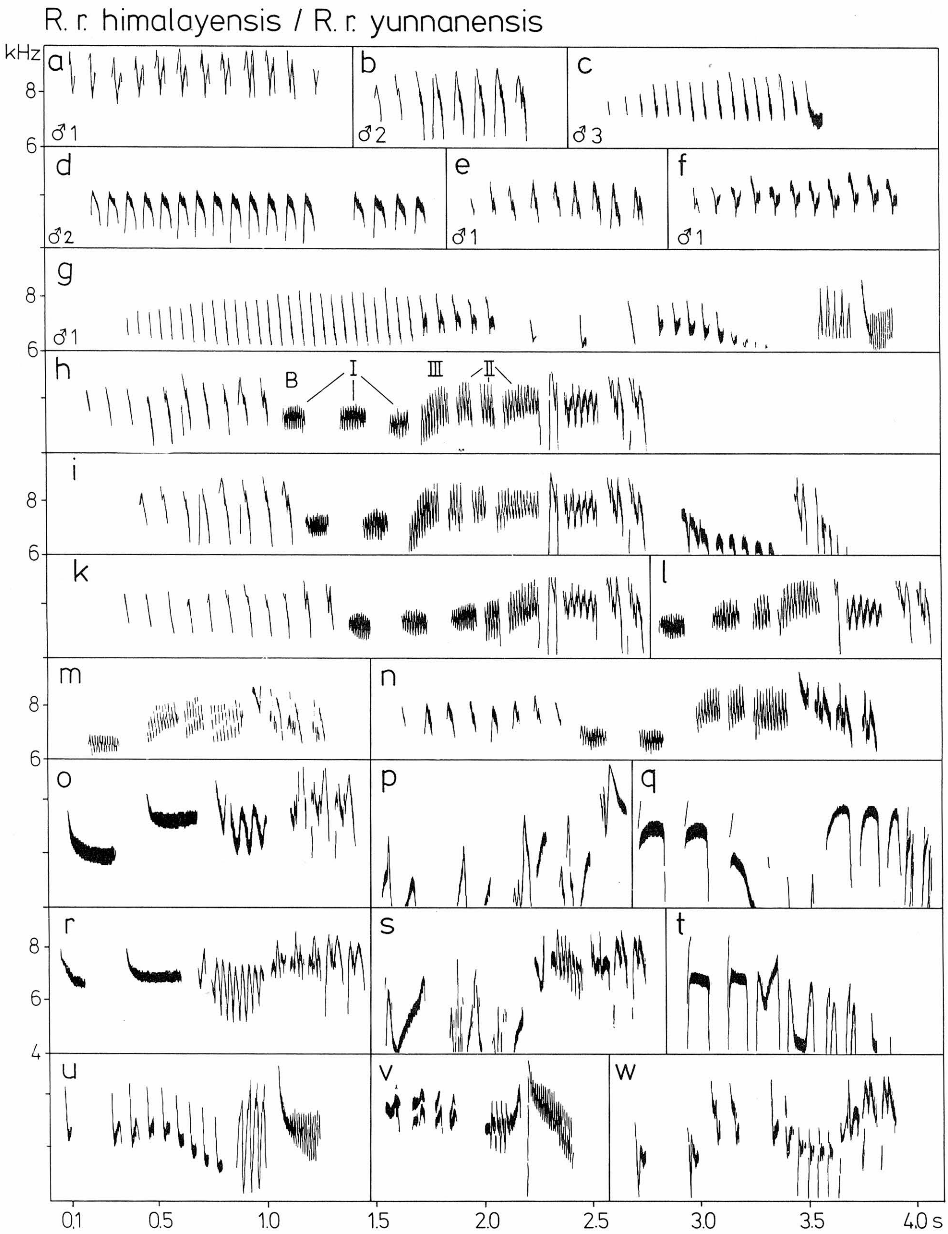

Fig. 5: Territorial song of *R. r. himalayensis* (a-c, h-l, o-q), *R. r. sikkimensis* (d-f, n, r-w) and *R. r. yunnanensis* (g, m). - a-c) *himalayensis* trills of territorial song main parts (Nepal); d-f) *sikkimensis* trills of territorial song main parts (China, Qinghai Prov.); g) *yunnanensis* full song; h-l) *himalayensis* full songs to show near-identical song types including B elements of different ♂♂ from various local populations (Nepal, Dhaulagiri area); m) *yunnanensis* B phrase; n) *sikkimensis* B phrase to show variation of B elements (in m trill part omitted); o-q) *himalayensis* song final parts of 2 ♂♂ (Nepal); r-t) *sikkimensis* homologous final parts of 1 ♂ (China, Qinghai Prov.); u-w) *sikkimensis*, additional final parts of the same ♂ (as in r-t; u may be a *Parus rubidiventris* call imitation).

rate in the main part: 18.8- 19.8 elements/s (*yunnanensis*) or 10.1-12.2 elements/s (*himalayensis/sikkimensis*). (Differences significant according to the Duncan test, $p < 0.05$).
The second characteristic of this territorial song, in addition to the introductory trill, is a sequence of call-like (B) elements, the syntax of which varies to different degrees (Fig. 5h-n). Every ♂ of all three subspecies is capable of singing this call sequence within the verse, but it is not an obligatory part of the verse. It may be added to the main, trill part, with or without a subsequent final part, but can also be performed in isolation, unconnected to a verse. The number of calls in the series is usually 5, but up to 7 in some ♂♂. When included in a verse it always comprises three types of call (Types I, II and III, Fig. 5h), which differ significantly from one another with respect to maximal frequency and pulse rate (analysis of variance and Tuckey test, $p < 0.05$ for the sequences of 5 B elements in *sikkimensis*). The verses in Fig. 5h-l illustrate the interindividual variation of B syntax in *himalayensis*.
There is a difference between *himalayensis* and *sikkimensis/yunnanensis* at the end of the B-element part: the *himalayensis* ♂♂ insert a complex element group there (Fig. 5h-l), which is lacking in the *sikkimensis* and *yunnanensis* songs.

Final parts: Size of repertoire 12 in one ♂ *himalayensis*, 4-5 in one ♂ *sikkimensis*, up to 8 per ♂ in *yunnanensis*; in 8 ♂♂ of all 3 subspec. a total of 26 observed. Although *himalayensis* and *sikkimensis* were recorded at sites about 2000 km apart, and their area cannot be continuously occupied for orographic reasons, we found consistencies in the repertoires of these two subspecies as well as that of *yunnanensis* (Fig. 5p-t). In the final parts of both populations C elements can be inserted (Fig. 5o,r); they are always present in certain types of final part (Fig. 5o,r), with frequency jumps between 6.6-6.7 and 6.7-7.0 kHz.

According to the available sample, the individual populations differ slightly from one another: *yunnanensis* has a higher trill rate in the main part than *himalayensis/sikkimensis*, whereas *himalayensis* differs from *sikkimensis/yunnanensis* in the structure of main-part elements, the shape of B elements and the final-part repertoire. However, these differences are small relative to the differences from other (disjunct) subspecies.
R. r. sikkimensis and *yunnanensis* are probably capable of incorporating vocalizations of the Simla Black Tit (*Parus rufonuchalis*) into the final parts (Fig. 5u; cf. MARTENS 1975: Fig. 10, 2nd row). Differences in pitch of the two vocalizations are obvious, however.

Regulus regulus tristis (Fig. 6)

Endemite of Central Asian mountain systems, chiefly in the Tian Shan.

Material: Kirghizia: Chatkalskij Ala Tau, Sari-Tshelek National-Park, 2 ♂♂, 98 songs, J. M. 29.-31.5.1993; - Issyk-Kul Basin, Terskej Ala Tau, SW Przewalsk (= Kara Kul), 1 ♂, 51 songs, J. M. 15.6.1993; - near Frunze (= Bishkek), 1 ♂, 7 songs, K. Mild 28.5.1987 (see MILD 1987). - In total: 4 ♂♂, 161 songs, 3 loc., 4 song types.

Auditory impression: Verse gradually increasing in volume, more agitated than that of all other subspecies, final parts audibly demarcated.

Call type	I	II	III	IV	V
			vt_2 / vt_3		
F_{max} (Hz)	7473	7436	7188 / 6946	7456 °	7344 °
^F (Hz)	512	1187	550 / 531	904	809
pulse rate	12,03	7,14	5,19 / 4,92	4,82	4,59

Tab. 2: Call types of *R. r. tristis*; ° = mean value of F_{max} of individual verses (vt_1 and vt_4); F_{max} = maximal frequency; ^F = frequency modulation; vt = verse type (see Fig. 7).

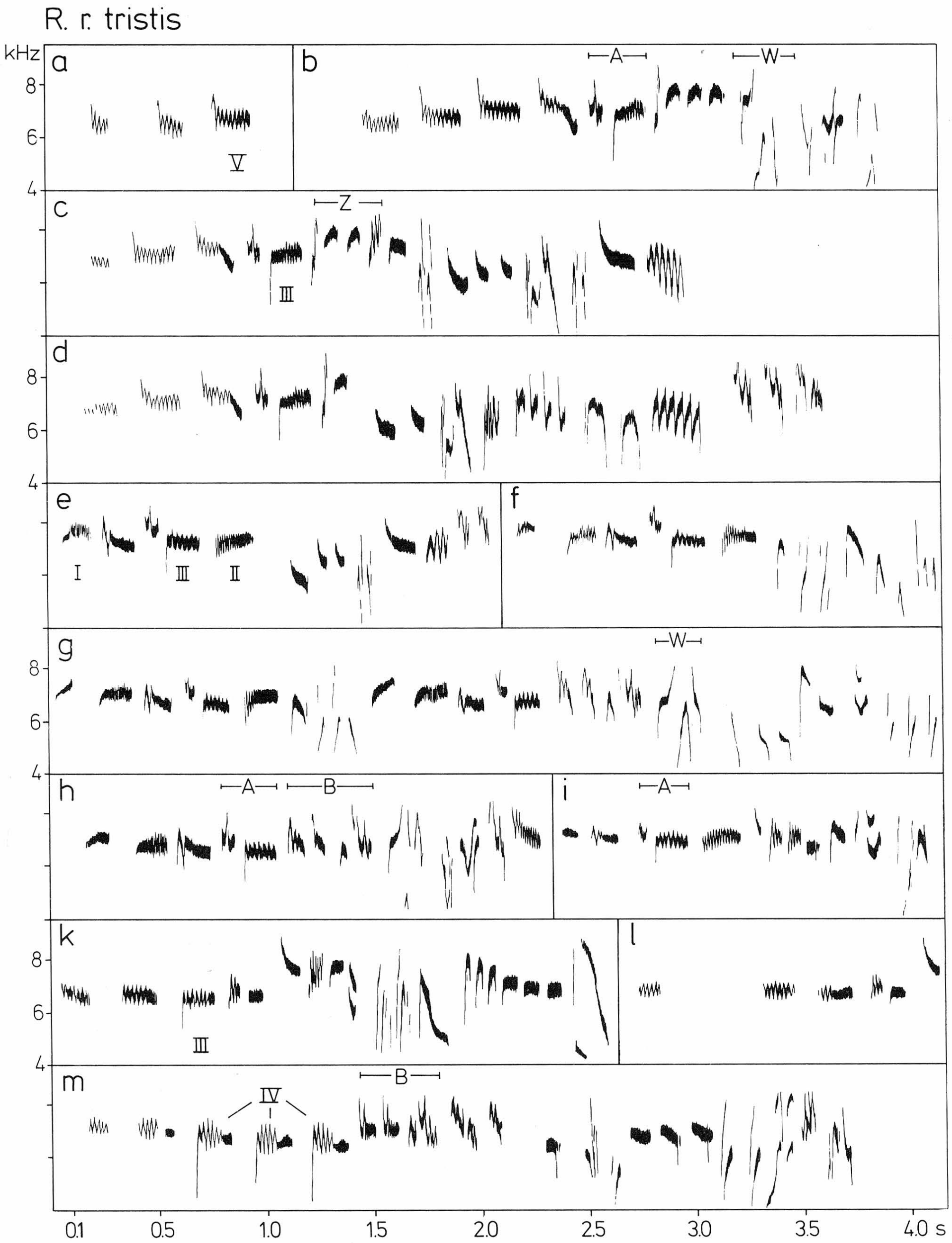

Fig. 6: Territorial song of *R. r. tristis* from various localities in Kirghizia (a-d: Sari-Tshelek; e- i: Issyk-Kul basin, Przewalsk; k-m: Frunze). - a-d) verse type 1 showing slight variation in element form and numbers; - e-i) verse type 2 (Issyk-Kul); k-l) verse type 3 (in l only main part shown; Bishkek); m) verse type 4 (♂ as in k-l); A, B and Z indicate stereotyped element groups which are inserted into various verse types at different positions. - W "weia" element group of German authors. See text for further explanation of letters. Call types I-V are indicated by Roman numerals (see Fig. 7).

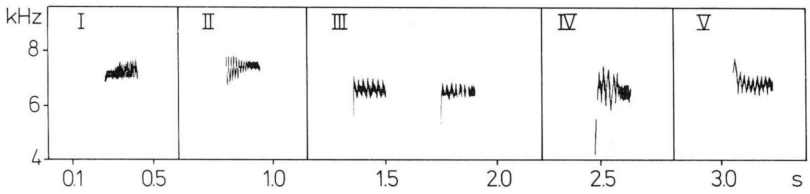

Fig. 7: *R. r. tristis*; examples of call types I-V, which are commonly used in main parts of the song.

Syntax: Verse structure very variable and extremely diverse (Fig. 6). The main part of the verse consists almost entirely of elements generally used by Goldcrests in different contexts as calls (B elements); they can be categorized as 5 types (examples in Fig. 7, Tab. 2) on the basis of maximal frequency, frequency modulation and pulse rate (analysis of variance and subsequent Tuckey test, $p < 0.05$). Each individual verse is dominated by element groups with B syntax, such as also appear in the *himalayensis* complex (cf. Fig. 5). Additional elements or element groups are also inserted, producing an extraordinarily complex syntax. Another peculiarity of *tristis* song is the "weia" motif (Fig. 5b, g, "W") in some final parts or at the very end of the verse, otherwise known only in *R. r. teneriffae* and *R. ignicapillus*.

Within the entire region investigated, we found 4 verse types, illustrated in Fig. 6. Most common are brief phrases composed of identical B elements with fundamental frequency that either remains constant (verse type 3, Fig. 6k-l, and 4, Fig. 6m) or rises (verse type 1, Fig. 6a-d). This B syntax is followed by a complex element group, the two together forming a stereotyped main-part unit. An element group may be incorporated into several verse types, at different positions (cf. A in Fig. 6 b and h). Verse type 2 (Fig. 6e-i) combines various call types with the element group A, to form a relatively complex unit. A certain element group „Z" (Fig. 6c) was also included in a closing part of the *japonensis* population in Hokkaido, nearly 6000 km away from the *tristis* area.

Final parts: Altogether 29 final parts were documented. Two ♂♂ of different populations (southeastern Issyk Kul basin and Sari-Tshelek) each had a repertoire of 18 final parts, 5 of which were the same in both.

Regulus regulus teneriffae (Fig. 8)

Endemite of the Canary Islands Tenerife, La Palma, La Gomera and El Hierro.

Material: Canary Islands, Tenerife, Anaga Mts., Mercedes Forest, 2 ♂♂, 28 songs, J. M. 14.3.1981.

Auditory impression: The comparatively short verse (up to 1.5 s) seems even shorter because the beginning is audible only in the immediate vicinity; final parts not much emphasized.

Syntax: Because the sample is so small, only general features are described here (with certain differences from BECKER 1978a, LÖHRL & THALER 1980). The main part contains several different elements, which can be combined with one another in various ways. In our material, two verse types can be distinguished (additional ones in BECKER 1978a, LÖHRL & THALER 1980).

Type 1 (Fig. 8a-b): An introductory trill with up to 20 short, slightly modulated A elements is followed by a group of several, variously strongly modulated elements; at the end is a

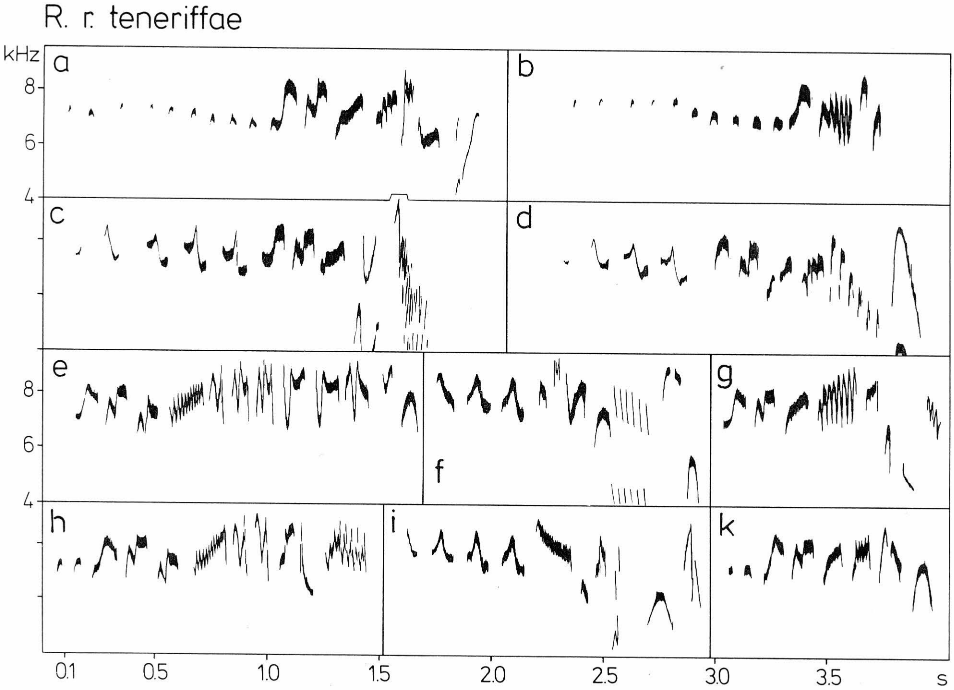

Fig. 8: Territorial song of *R. r. teneriffae* (Canary Islands, Tenerife). - a-d) different verse types of 1 ♂ (a-b with low initial trill); e-k) different verse types of second ♂.

variable final part. The trill is sung quietly and is not always immediately obvious in the sonagram. BECKER (1978a) did not describe it; cf. also LÖHRL & THALER (1980). Maximal frequency in the trill 7.7 kHz, minimal 7.2 kHz (^F = 0.5 kHz); trill rate 10.9-12.4 A elements/s (as in the *himalayensis* group).

Type 2 (Fig. 8 c-e, h): Phrase comprising basically A-type elements, but longer and more richly structured, followed by an element group like that in Type 1 and a final part.

F i n a l p a r t s: In both verse types these usually cover a larger frequency band than the preceding parts of the verse; each ♂ sings several final parts (13 in the case of one ♂, 19 for both together). BECKER (1978) found 21 final parts in 29 different verses, only a few of which were the same in two or more ♂♂. Most ♂♂ combined elements to form final parts specific to that individual.

Regulus satrapa

A Nearctic species of *Regulus*, 4 subspecies are distributed from S Alaska to Mexico and W Guatemala, and as far east as Newfoundland and Nova Scotia.

M a t e r i a l: *R. s. satrapa*: Algonquin Provincial Park, Ontario, Canada, 2 ♂♂, 10 + 11 songs, Tom Cosburn, 21.+27.5.1988; Bark Lake, Ontario, Canada, 1 ♂, 8 songs, W.W.H. Gunn, 20.6.1971. - *R. s. olivaceus*: Cornox Valley, Vancouver Island, Canada, 1 ♂, 3 songs, Douglas Innes, 12.6.1990 (all by courtesy of National Sound Archive, London).
Series of incomplete songs and subsong-like vocalizations, all recorded from captive *R. s. satrapa* transferred from Ontario, Canada, to Austria as subadults, by E. Thaler.

	japonensis-1	*japonensis*-2	*himalayensis*	*tristis*	*teneriffae*	*regulus*
t	2,56	3,03*	2,36	2,8	1,63*	2,73
F_{max}	7,75	7,93	8,6*	8,2	8,01	8,2
F_{min}	6,1	5,06*	6,9	6,26	6,71	4,72*
^F	1,65	2,87*	1,69	1,94	1,3	2,56*
z	2	1	1	>5	>5	4(5)

Tab. 3: Measurements of various verse parameters of *R. regulus* of song.
Japonensis-1 = Russian Far East population; *japonensis*-2 = Hokkaido population; *himalayensis* includes *himalayensis, sikkimensis* and *yunnanensis*.
t: verse length (s); F_{max}: maximal frequency (kHz); F_{min}: minimal frequency (kHz); ^F: frequency bandwidth (kHz); z: number of main part elements; *: indicates significant difference to all other subspecies (Mann Whitney U test: $p < 0,05$); mean values calculated from n = 28 (*teneriffae*) to n = 275 (*japonensis*/Russia) verses.

Auditory impression: Uniform whistling song, rising in pitch, with clearly demarcated final part.

Syntax: The 4 ♂♂ in the field sang the same type of verse. The main part is a series of whistles (C elements) ascending from 7.2 to 8.2 kHz; in one ♂ the series was lower-pitched, beginning at 6.7 kHz. It comprises up to 7 C elements (Fig. $12f_1$) and may be followed by a phrase made up of more strongly frequency-modulated whistles (similar to a call: Fig. $12f_2$). The main part can thus consist of one or two phrases. A verse of this type was illustrated by BECKER (1978).
The song of ♂♂ caught as juveniles in autumn and raised in captivity (THALER 1990b) had a subsong-like character. Some consisted of brief verses with whistle or call phrases, to which was attached a final part, but others were sequences of C whistles like those of the free-living ♂♂, in either ascending or irregularly alternating syntax, plus call series and final parts.

Final parts: In the 32 verses recorded from four ♂♂ in the field, which belong to the subspecies *satrapa* and *olivaceus*, only one final part was present and sung identically by all ♂♂ (Fig. $12f_1$, f_2).

Comparisons between the subspecies

In this section, important characters of the songs of various major populations (in the sense of subspecies or groups of subspecies) are compared with one another (cf. Table 3). In addition to the general structure of the verse, these include the minimal and maximal frequency, the frequency modulation of the elements in the main part, and the length of the verse. The differences were tested for significance, initially by analysis of variance (main-part structures more or less normally distributed) and then by means of Mann Whitney U test that is more suitable for small samples. The main-part structures of all subspecies are shown in Fig. 9.
According to these tests, *regulus* song has the lowest pitch, the *himalayensis* complex the highest. There are practically no subspecific differences in length and frequency bandwidth of the verses, so that these parameters must be regarded as relatively constant characters. The divergence of other characters among the subspecies varies in degree. Some subspecies are quite isolated by (as many as three) highly divergent syntactic characters: *regulus* by ^F and F_{min}, *japonensis*/Hokkaido by ^F, F_{min}, and verse length, the *himalayensis* group by F_{max}, *teneriffae* only by verse length.

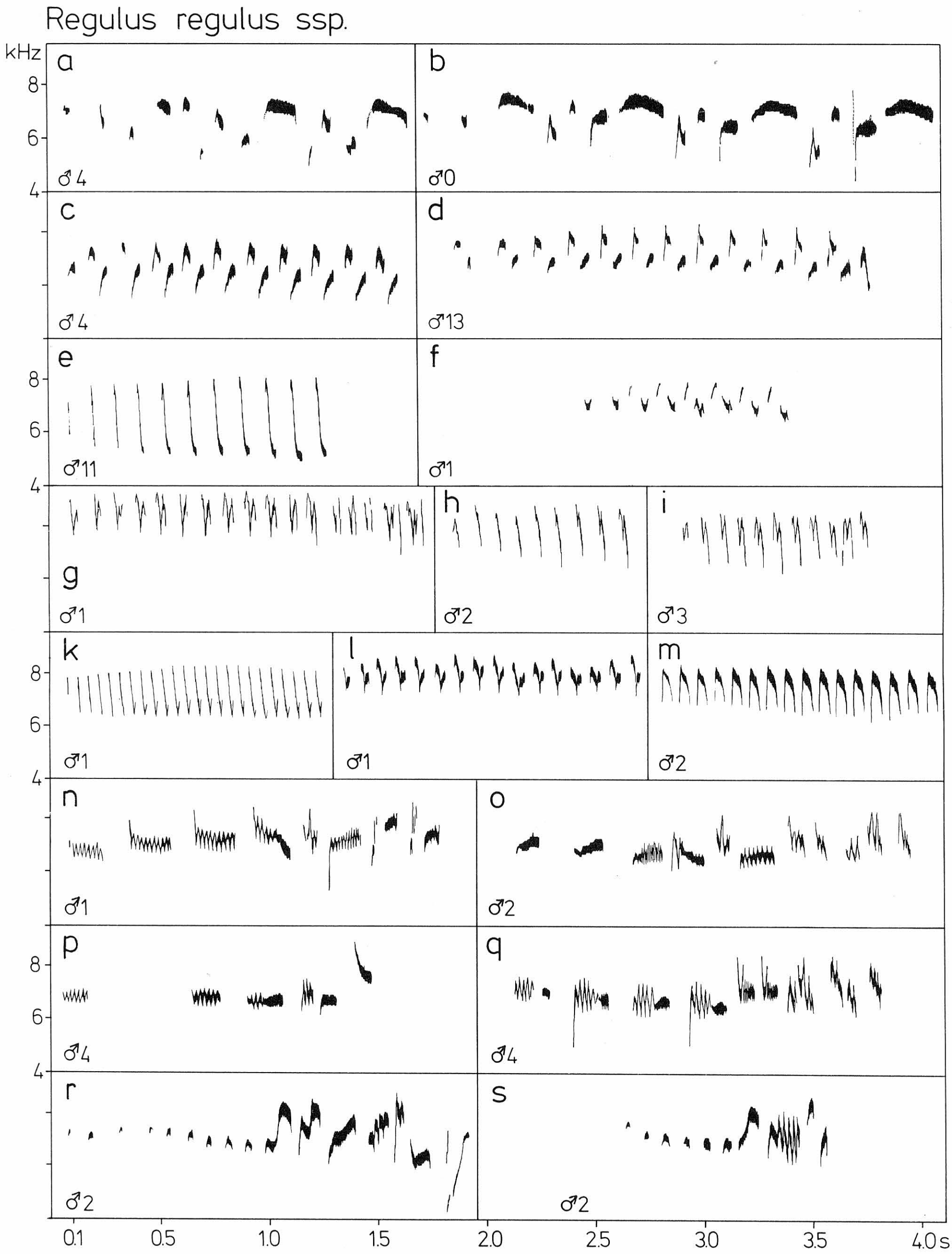

Fig. 9: Comparison of main parts of the song of various *R. regulus* subspecies, with respect to the chief song characteristics.
I; a-d, f) Repetition of element groups including frequency jumps; - a-b) *R. r. regulus*, c-d) *R. r. japonensis*; from Russian Far East (c-d) and Honshu (f).
II; e, g-m) Main part divided into trills and phrases (only trills shown); e) *R. r. japonensis*/Hokkaido, g-i) *R. r. himalayensis*; k) *R. r. yunnanensis*; l-m) *R. r. sikkimensis*.
III; n-s) Complex structure of main song part, with widely varying composition of elements. - n-q) *R. r. tristis*; r-s) *R. r. teneriffae*.

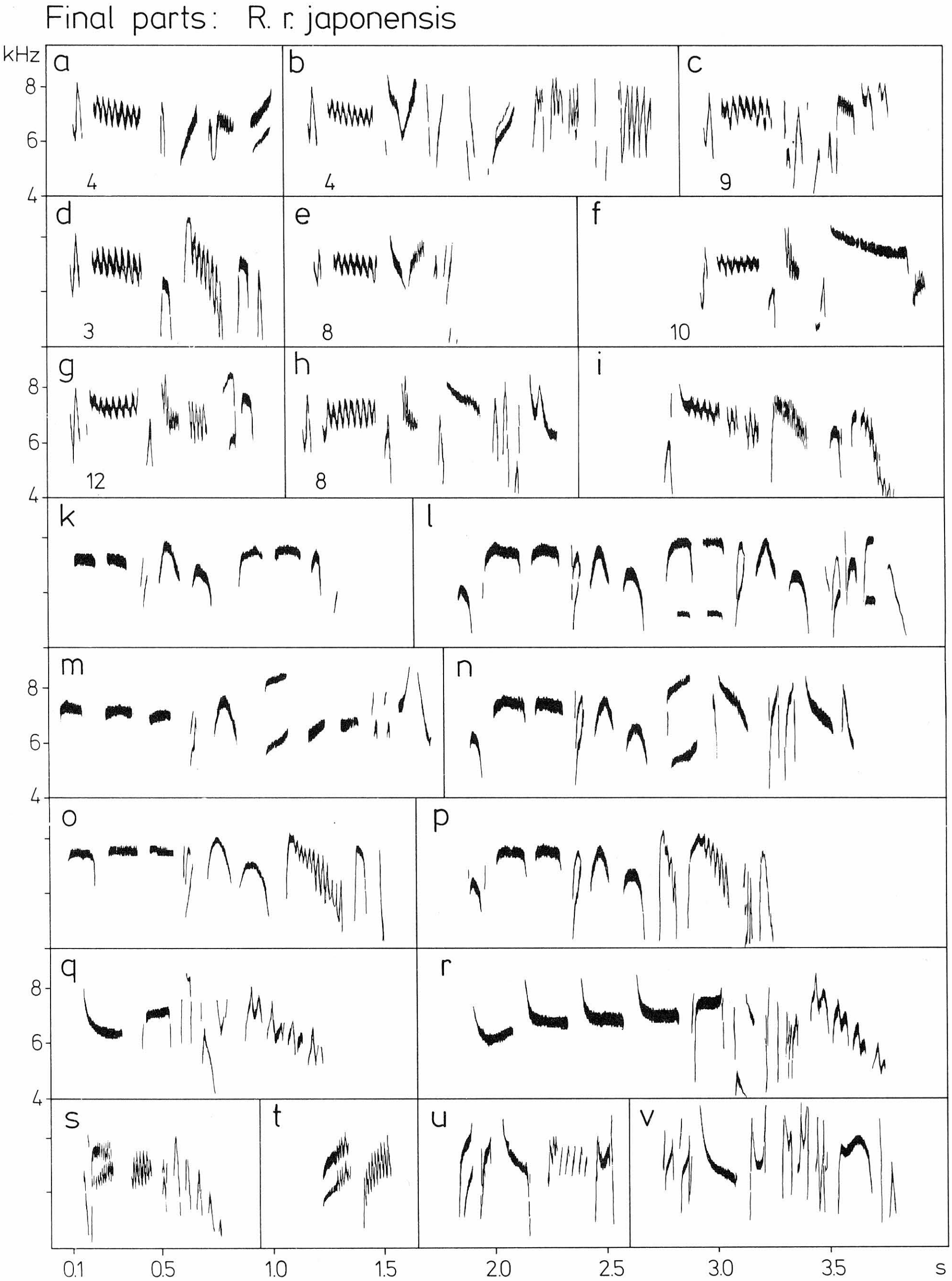

Fig. 10: Comparison of final parts of the songs of *japonensis* populations in the Russian Far East (3 localities; a–e, k, m, o, q, s, u) and Japan/Hokkaido (1 loc.; f–i, l, n, p, r, t, v) to show strong similarities between widely disjunct populations. - Final parts a–e (Russia) and f–i (Hokkaido), all belonging to the same type, show extreme inter- and intra-individual variation.

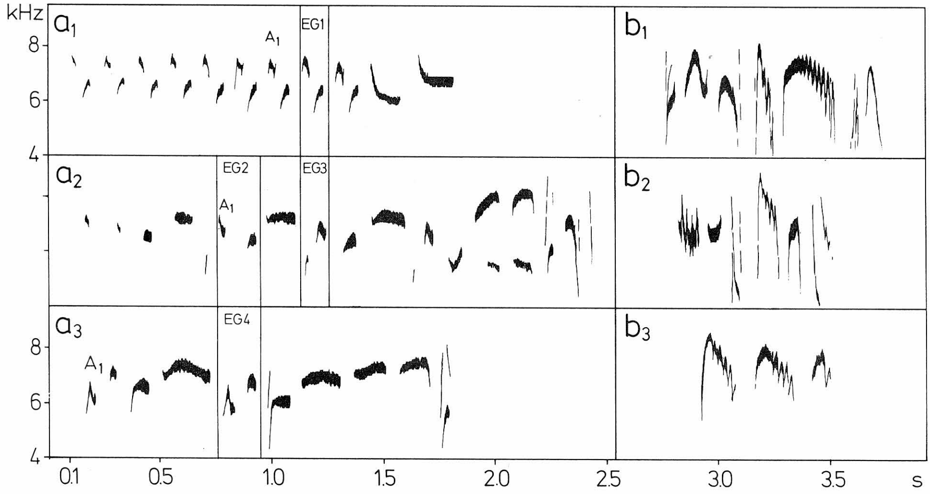

Fig. 11: a_1-a_3: Comparison of element groups of main parts in *R. r. japonensis* and *R. r. regulus* song. EG_1 and EG_2 are probably homologous structures. a_1: *japonensis* Russian Far East, a_2, a_3: *regulus* Taunus Mts, SW Germany. - b_1-b_2: imitations of *Parus palustris* incorporated into song final parts of b_1) *R. r. japonensis* (Russian Far East), b_2) *R. r. regulus* (Taunus Mts.), b_3) *Parus palustris* calls, Cévennes, SW France (b_3 rec. by C. Uhle).

An intra-subspecific comparison: *R. r. japonensis* in the Russian Far East and Hokkaido:

The sonagram analysis in itself revealed differences and common features of the two *japonensis* populations in the Russian Far East and Hokkaido (Figs. 3 and 4). Additional important characters are found in the structure and extent of the final-part repertoire (Fig. 10). We found 6 final parts in both regions and, although these differed slightly from one another, they were sufficiently similar to be considered homologous (Fig. 10). Most of these 6 final parts are very frequently used: 4 of them are sung by over 60 % of all individuals, and 3 by over 50 % of the individuals in Russia.

Comparison between *japonensis* and the *himalayensis* group:

In 2 final parts, individual element groups (Figs. 12c-e) were the same in *japonensis* song (Russian Far East and Hokkaido) as in the songs of all 3 subspecies of the *himalayensis* group. One of these final parts (Fig. 10a-i) is the only one within the *himalayensis* group that comprises a series of ascending C elements - a striking character of *japonensis*! This final part (Fig. 10a-i) was actually used by every ♂ observed in Russia.

Comparison between *japonensis* and *regulus:*

Main part: Only the Russian (and Honshu) populations of *japonensis* and the nominate form *regulus* repeat one element group regularly in the main part of the verse. This group comprises 2 elements in *japonensis* (Fig. 11a_1), 4-5 in *regulus* (Fig. 11a_2, a_3). Comparison of this element group in *japonensis* and in two corresponding groups of *regulus* (Fig. 11a_1-a_3) reveals the following.
Points of agreement: EG_1 (*japonensis*) and EG_2 (*regulus*) are the same with respect to the shape of both elements, the frequency range of the element group and the magnitude of the frequency jump between the elements (Duncan test, $p < 0.05$).

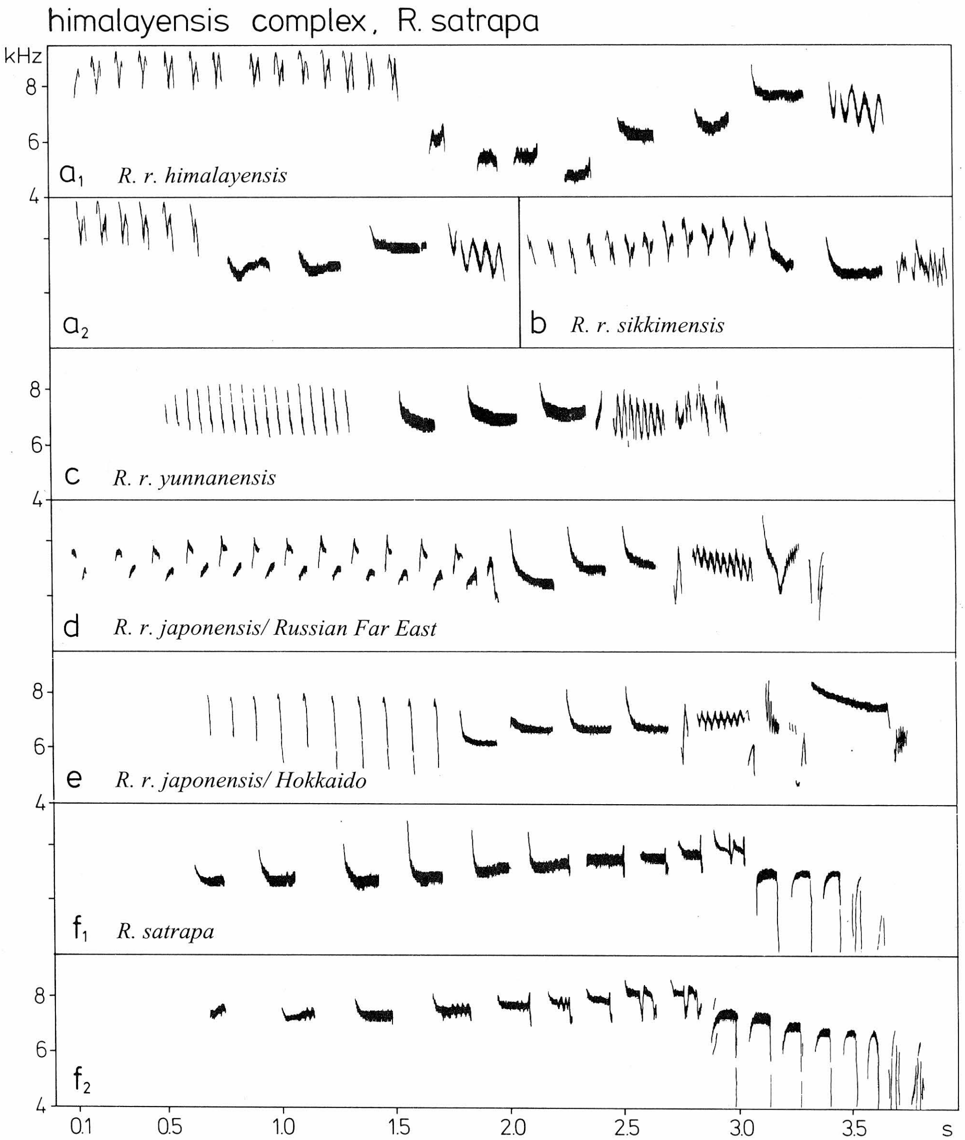

Fig. 12: Full territorial songs of various *R. regulus* subspecies to show clinal enlargement of C-element groups (whistles) from the Himalayan region to China, Japan and N America. - a_1-a_2) *himalayensis* (Nepal), b) *sikkimensis* (China, Qinghai Prov.) c) *yunnanensis* (China, Shaanxi Prov.); d) *japonensis*, Russian Far East; e) *japonensis*/Hokkaido; f_1-f_2) *R. satrapa* (Canada, Ontario).

Differences: These relate to the temporal separation between the two elements in the group, which varies widely in *regulus*: the element groups of certain ♂♂ are like those of *japonensis* but others are quite different ($p < 0.05$). The comparison is affected by the way the main part of *regulus* song is subdivided into element groups (whether A_1 is combined with the preceding or the following element). Furthermore, the maximal frequency of the

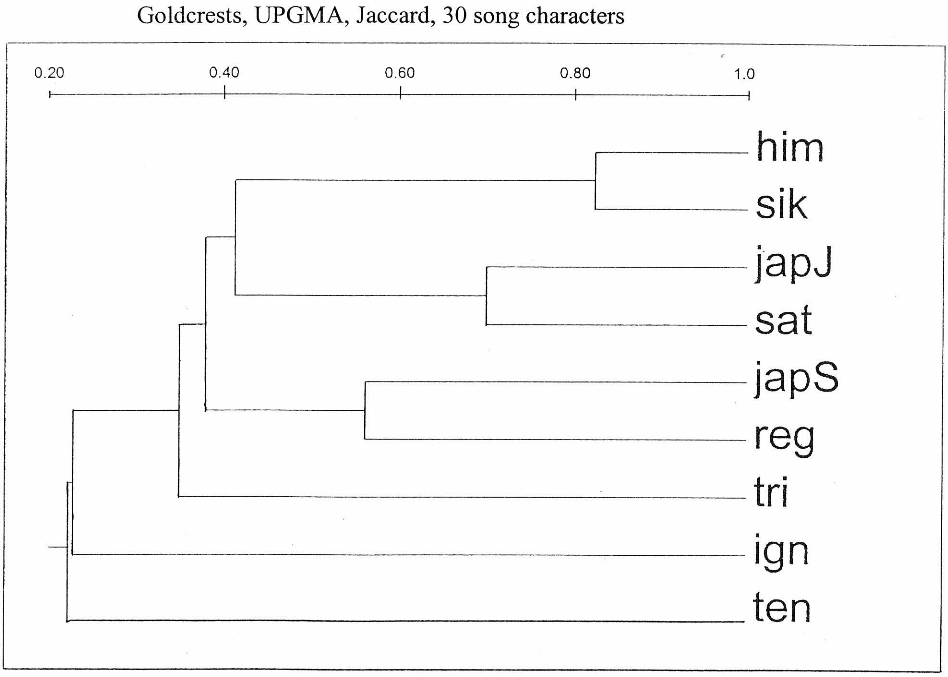

Fig. 13: UPGMA analysis of 30 different song characteristics of various *R. regulus* subspecies plus *R. ignicapillus* and *R. satrapa*. (Phenogram does not represent the phylogeny of the *R. regulus* / *R. ignicapillus* / *R. satrapa* complex, but indicates song similarities between taxa).

two elements differs ($p < 0.05$, Duncan test), being on the whole lower in *regulus* as is consistent with the generally lower pitch of the *regulus* verse.

C-element sequence (Fig. 12)

The number of C elements differs among the three eastern Asian populations (not counting *tristis*, which lacks a C-element sequence). We distinguish 9 types of C-element sequence, according to the number of C elements (1-9) that can be present in a verse. Within the *himalayensis* complex C elements appear only in certain final parts; in the Russian Far East there are usually only 1 or 2 C elements, whereas in Japan sequences of 3-9 C elements predominate (frequency jumps within the sequence are described above). Each ♂ has in his repertoire verses with various numbers of C-element components.

The verse of the Nearctic *R. satrapa* includes in the main part a uniformly ascending sequence of C elements (Fig. 12f_1, f_2), like that of the eastern Asian *R. regulus* subspecies. Frequency jumps are less conspicuous than in the song of *R. r. japonensis* on Hokkaido, and the whistle sequence as a whole is somewhat higher-pitched (up to 8.2 kHz).

All the eastern Asian representatives of *R. regulus* exhibit striking frequency jumps in the range from 6.2 to 7.0 kHz (Fig. 12). Jumps of similar size (from 6.2 kHz to 6.6 kHz or from 6.6 kHz to 6.8 kHz) are found in the *himalayensis* group as well as in both the continental and Hokkaido populations of *japonensis*. In the upper region of the common frequency spectrum the whistle sequence of *R. satrapa* shows similarities with that of the eastern Asian representatives of *R. regulus* (6.7-7.7 kHz).

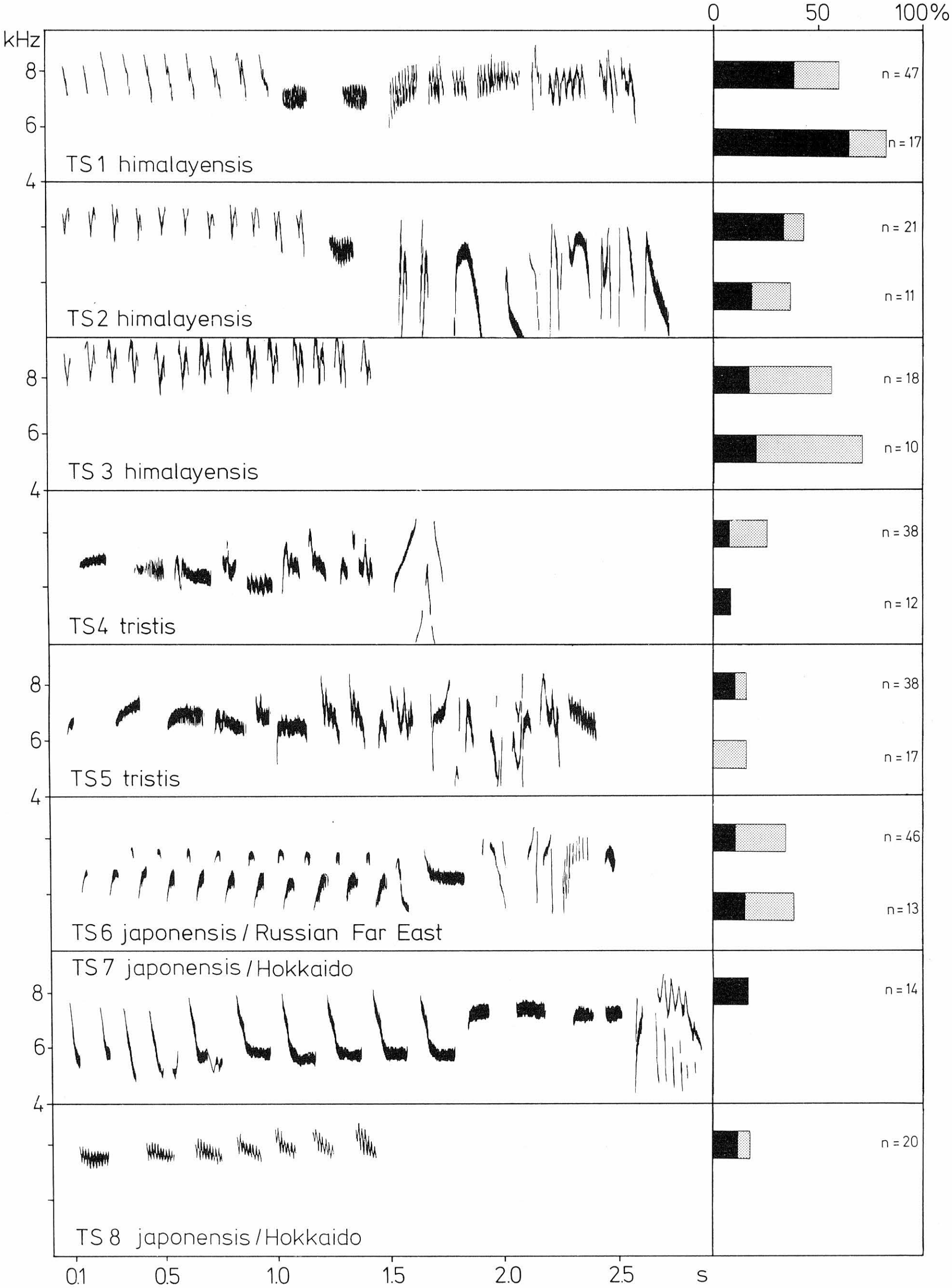

Fig. 14: Results of playback experiments with various test songs of *R. regulus* subspecies, carried out near Taunusstein/SW Germany. Goldcrests (*R. regulus*) and Firecrests (*R. ignicapillus*) were tested (upper and lower bars, respectively). Test songs originate from Nepal (TS 1-TS 3, [in 3 only trill part]; *himalayensis*); Kirghizia (TS 4-TS 5; *tristis*); Russian Far East (TS 6; *japonensis*); Hokkaido (TS 7, TS 8 [call series in 8]; *japonensis*). - Numbers of tested individuals are indicated. Black: strong territorial reaction, light: weak territorial reaction. - TS test song.

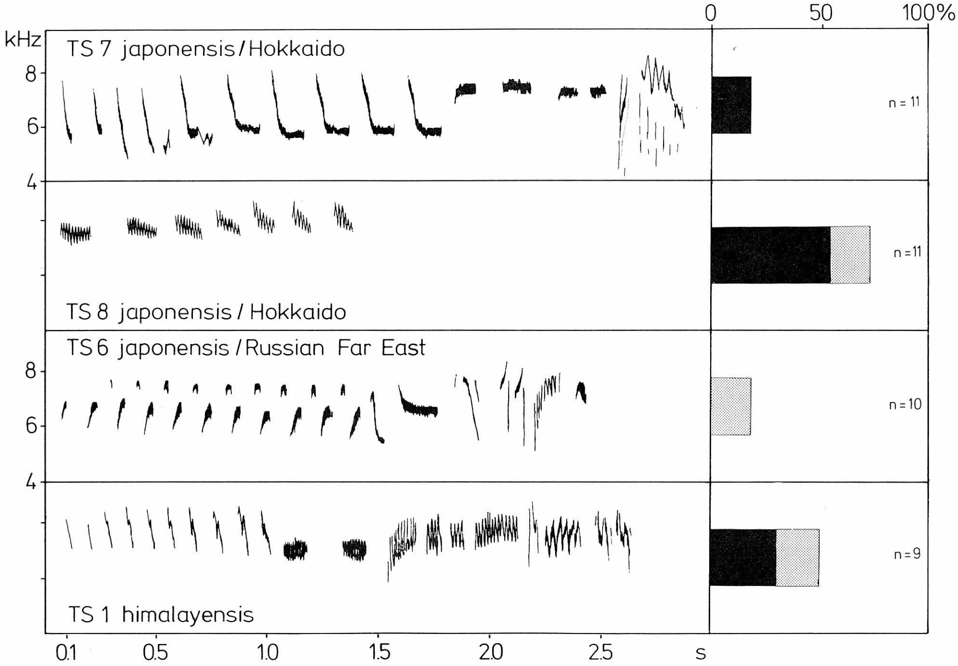

Fig. 15: Results of playback experiments with various test songs carried out in Ussuriland, Russian Far East (TS 7, TS 8; *japonensis*/Hokkaido) and in Hokkaido (TS 6: *japonensis*/Russia, TS 1: *himalayensis*/Nepal). - For intensities of reaction see Fig. 14.

The whistle sequences of *R. satrapa*, thus, resemble those of the *himalayensis* group and the *japonensis* populations with respect to form of element, ascending phrase syntax and even the details of the frequency jumps between consecutive C elements.

Structural relationships

A more detailed picture is obtained when the various characters distinguishing the main parts of the verses of all the subspecies considered here are analyzed by UPGMA. The graph in Fig. 13 includes 30 different main-part structures of all subspecies. This cladogram indicates relative similarities in the songs, and does not imply phylogenetic conclusions. Characters we regard as derived, however, do at least provide some clues to the phylogenetic relationships.
A striking feature is that not only *R. ignicapillus* but also *teneriffae* clearly stands out from the other *R. regulus* forms. Furthermore, it is evident that *tristis* is quite isolated acoustically. *R. satrapa*, on the other hand, although not ordinarily considered a form within the *R. regulus* complex, is closely associated with the geographically closest form, *japonensis*/Hokkaido, with only slight differences. The geographically more distant continental *japonensis*/Siberia is separated from these by divergent element and syntax forms.

Playback experiments (Figs. 14, 15)

R. regulus in SW Germany: Goldcrests here in general gave significantly weaker responses to the recorded songs of other populations than to the control songs of conspecifics recorded locally. Comparisons showed that the *himalayensis* test songs 1 and 2 were understood better by the Goldcrest (and by the Firecrest) than the other test songs. Responses to the test song 3 of *himalayensis* were barely above the significance level (Man Whitney U test; $p > 0.05$). Test songs 1 and 2 were not significantly different in their effects on either Goldcrest or Firecrest. Evidently, then, it is unimportant whether the verse contains a call sequence or not. Firecrests actually responded more strongly than Goldcrests to test song 1 of *himalayensis* (significance level only slightly exceeded: $p = 0.0509$); in fact, its response was not significantly different from that to the conspecific control song.

R. r. japonensis on Hokkaido: The song of the Russian *japonensis* elicited almost no response (Fig. 15, ca. 10 %). Here, again, no significant difference was discernable between *himalayensis* song (Fig. 15, TS 1) and the local song used as a control. The reason may be that the response to the control was comparatively poor, probably because the syntax of the control verse was not typical of the test site (Fig. 8m).

In Russia: The *japonensis*/Hokkaido test song was understood here distinctly less well than the typical local song ($p < 0.05$). However, vigorous responses were elicited by the Japanese call series, no different from those elicited by local song (Fig. 15).

According to these field experiments, the continental and Hokkaido *japonensis* populations are clearly isolated by their territorial songs, but not by the call series.

In China, *sikkimensis* and *yunnanensis* gave vigorous, aggressive responses to *himalayensis* song.

Discussion

The song structures of the passeriform suborder Oscines have been thought not to be particularly helpful for phylogenetic investigation, because they are learned (KROODSMA et al. 1996). It has been said that they have large intraindividual variability and that evolutionary trends are likely to be rapidly concealed by marked "cultural mutation" (JENKINS 1978; LYNCH 1996). Here we shall examine these objections in the light of our results.

Song structures and distributional areas

We have shown that the verse syntax of all *R. regulus* subspecies is not fully represented by that of the W Palearctic *R. r. regulus* (BECKER 1977a, CRAMP 1992) and that of the Canary Island subspecies *R. r. teneriffae* (BECKER 1978, LÖHRL & THALER 1980): the various Asian subspecies add still more versions. In each of the large parts of the species' area in central and eastern Asia distinct song forms exist, each with little variation. That is, the Goldcrest is a species with notable regiolects (MARTENS 1996). Because of the strict geographic limitations of regiolects, each is closely associated with populations traditionally identified by subspecies names; the distribution of a regiolect is usually identical with that of a particular subspecies that sings this song form. The *himalayensis* complex (subspec. *himalayensis, sikkimensis* and *yunnanensis*) is an exception. Its populations merge with one another with no sharp boundaries (VAURIE 1959), and they represent a unitary regiolect region. Accordingly, *sikkimensis* and *yunnanensis* give strong responses to *himalayensis* song. In contrast, the *japonensis* area has proved, unexpectedly, to be subdivided into two regiolect regions, the far eastern part of continental Russia plus the island of Honshu on one hand, and Hokkaido on the other.

Within these subdivisions of the species' area, including Europe, the songs do not vary randomly: relationships can be discerned and sometimes appear as distinct character progressions (clines). When viewed in this way, three categories of *R. regulus* song emerge (Fig. 16). (i) Tian Shan (*tristis*) - Himalayas/China (*himalayensis* complex): These two population

I. Initial state of song (hypothetical): subsong-like, different song-parts, various combinations

A phrase: ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧

B phrase: w w w w w w w w w

C final part: _ _ W)))

loss of A → ***R. r. tristis***

only main part: B phrase (complex combination)

w W w w w w W w W w

song like in I. (relictual state) → ***R. r. himalayensis***, ***R. r. sikkimensis***, ***R. r. yunnanensis***

II. Intermediate state (hypothetical, evolved from I.): loss of B phrase, phrase of C elements incorporated into main part

A phrase: ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧

C phrase: _ _ _ _

final part: W)))

(to bottom only main parts are figured)

main part consisting of element groups, 2 elements per group → ***R. r. japonensis***/ Russian Far East

A groups: ^^ ^ ^ ^ ^ ^ ^ ^ ^ ^ ^ ^ ^

C phrase (short): _ _

prolongation of C phrase → ***R. r. japonensis***/ Hokkaido

A phrase (short):))))))

C phrase (long): _ _ _ _ _ _

loss of C phrase, final part often starts with B elements; element group consists of 4-5 elements → ***R. r. regulus***

A groups: ∧ ∧ ∧ ∧ ∧ ∧ ∧ – ∧ ∧ , – ∧ ∧ , – ∧ ∧ , – ∧ ∧ , –

[B phrase (short)]: W W

loss of A phrase → ***R. satrapa***

C-phrase (long): _ _ _ _ _ _ _ _

R. r. teneriffae: secondary A-element trill, complex element group at the end

A phrase (trill + element group): ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧ ∧ √ γ ∫ –

[B phrase (short)]: w w

groups both integrate into the verse strongly frequency-modulated ("pulsed") B elements, very similar to the innate calls (BECKER 1978b, THALER 1990a for *R. ignicapillus*). Furthermore, both groups include occasional C elements, although only in a few types of verse. The verse of *tristis* lacks a distinct introductory component (A phrase, Fig. 16); it may have been lost by drift, given the extremely small population sizes in the Tian Shan refugial region (cf. NAZARENKO 1990).
(ii) Himalayas/China (*himalayensis* complex) - Russian Far East/Japan (*japonensis*): The whistle (C) elements of the verse in the *himalayensis* complex clearly become more numerous in populations living further east. They are incorporated into either the final part (*himalayensis* complex, Fig. 12a-c) or the main part (*japonensis*, Fig. 12d-e). The gradation is discernible even within *japonensis*, from the Pacific coast of Russia to the Japanese islands. The longest C sequences were documented on Hokkaido. Remarkably, this trend is continued by *R. satrapa* in N America. The main part of the *satrapa* verse consists exclusively of C elements and lacks the introductory elements that are always present in all *japonensis* verses (Figs. 3, 4, 16).
(iii) Russian Far East (*japonensis*) - Central Europe (*regulus*): The main part of the verse is dominated by element groups comprising 2 (*japonensis*) or 4-5 elements (*regulus*; in central France there are also dialect forms with only 2 elements per group: BECKER 1977a), with distinct frequency jumps between the elements. C-element (whistling) phrases have not been found in any population of *regulus*. *R. teneriffae* uses a highly derived variant of the *regulus* song (see below).

This triple subdivision of the *regulus* songs simultaneously implies a phylogenetic series. We regard songs with many call elements (*tristis, himalayensis* complex) as primitive, close to the proto-*regulus* song. Songs of the *himalayensis* complex (but not those of *tristis*) have a clearly demarcated trill at the beginning of the main part of the verse, probably a derived structure. The whistling C-element phrases are increasingly emphasized in a W to E progression that begins with the *himalayensis* complex, continues within *japonensis*, and even includes the Nearctic *R. satrapa*. In the remainder of the area, in N Asia and Europe, the nominate form represents a derived (and comparatively young) song form in which the C elements have been replaced by a main part of complex structure. The UPGMA analysis (Fig. 13), which is based entirely on song characters, reflects this interpretation.

Evolutionary history of songs

The extremely fragmented transpalearctic area of the Goldcrest, together with striking morphological and acoustic differentiations, indicates a complicated history of dispersal and evolution (VOOUS 1962).

R. regulus:
The proto-Goldcrest is most likely to have originated in Palearctic Asia, in the region of present-day China. The songs of *tristis* and the *himalayensis* complex include ancient characters, and the slight development of the crown stripe in *tristis* may be a primitive morphological character. The present-day *japonensis* populations, living at the edge of the Pacific, are derived from such central Asian populations. Within *japonensis* the population on Hokkaido has certainly been isolated for a long time, during which it was occasionally reduced to a small number of individuals. The acoustic differences between the Russian Far East/Honshu and Hokkaido are striking; no morphological differences have yet been documented.

◀
Fig. 16: Scheme of the hypothetical song evolution of the *R. regulus* complex. This graph assumes that *R. satrapa* is a close relative of *R. regulus* (see Discussion). A, B and C phrases consist of the corresponding element types (cf. Figs. 3a, 5h).

This scenario implies that the Goldcrests of the W Palearctic are comparatively recent. Acoustically the nominate form can be derived from the form in the Russian Far East (*japonensis*; cf. Figs. 3 and 11a). A key role here may have been played by the W Siberian subspecies *coatsi*, which is in contact with nominate *regulus* (Fig. 1) but for which no tape recordings are available. According to JOHANSEN (1952) and CRAMP (1992), this form is closely related to *japonensis*; this situation would presumably be reflected in its song.

Populations of the Atlantic Islands:
There are no old relict populations of *R. regulus* in the W Palearctic; even the area splinters on the Canaries and Azores are comparatively young. According to the sonagrams published of Azorean Goldcrests (*R. r. azoricus, R. r. inermis*) (KNECHT & SCHEER 1971) these produce song types typical for nominate mainland *R. r. regulus*. Whereas the Goldcrests of the Azores have always been counted as *R. regulus*, the position of *teneriffae* is less clear. So far the discussion has centred on four possibilities: that it is a form of *R. ignicapillus* (VOLSOE 1951, according to acoustic characters; VAURIE 1954, 1959) or of *R. regulus* (BECKER 1978, CRAMP 1992, ECK 1996), a separate species (WOLTERS 1980), or an (extremely old) allospecies of a superspecies *R. [regulus]* (LÖHRL & THALER 1980, SIBLEY & MONROE 1990, GLUTZ V. BLOTZHEIM & BAUER 1991). To judge by its song structure (subdivision into a main and a final part) and certain call types, *teneriffae* is clearly a representative of *R. regulus* (BECKER 1978). The distinct acoustic (and morphological) differences in detail from all other *regulus* forms (short verse length, several verse types per ♂, many and variable element types) we explain by drift. That is, the islands are likely to have been colonized only by small groups of individuals, which brought with them few of the acoustic characters of the whole repertoire and then proceeded to develop these few characters on the islands. In Spain, close to the area border of nominate *regulus*, BECKER (1977a) found verse types that closely resembled those of Tenerife. Developments in the evolution of the *regulus* complex have been widely spaced in time, and among them the splitting off of *teneriffae* is a relatively recent event, likely to have occurred during one of the last interglacial stages. STURMBAUER et al. (1998) found only a single point mutation in the quite conservative 16SrDNA between Central European *regulus* and *teneriffae*. This clearly indicates their extremely close relationships. ECK (1996) emphasizes that the western (including *teneriffae*) and the eastern Palearctic subspecies can readily be distinguished metrically! We therefore consider that there are insufficient grounds for granting *teneriffae* species status.

Interspecific relationships

In order to illuminate the relationship between *R. regulus* and *R. satrapa*, all the larger *Regulus* taxa must be considered. Two interpretations suggest themselves (Fig. 17), both incorporating morphological as well as acoustic characters. In both of them *R. calendula* is taken to be a very old form of *Regulus*, occupying a near-basal position and at present no longer having any close relatives. This idea is corroborated by the data taken from the 16SrDNA analysis (STURMBAUER et al. 1998).

Hypothesis 1 (cf. Fig. 17a): A bipartite song with final part is a primitive character. The "eyestripe firecrests" (*R. ignicapillus, R. goodfellowi, R. satrapa*) are monophyletic and constitute the sister group of *R. regulus*; their common origin is indicated by the eyestripe (though only weakly developped in *R. goodfellowi*). This term („Augenstreif") with respect to systematics was first mentioned by KLEINSCHMIDT (1913). *R. ignicapillus* and *R. goodfellowi* have discarded the final part of the originally bipartite song (*R. goodfellowi* song in the National Sound Archive, London). In fact, the song of *R. ignicapillus* may have had two parts, counting the "weia" motif (BECKER 1978a, THALER 1990a). The ascending series of C elements, shared by *R. satrapa* and the far eastern forms of *R. regulus*, must therefore be

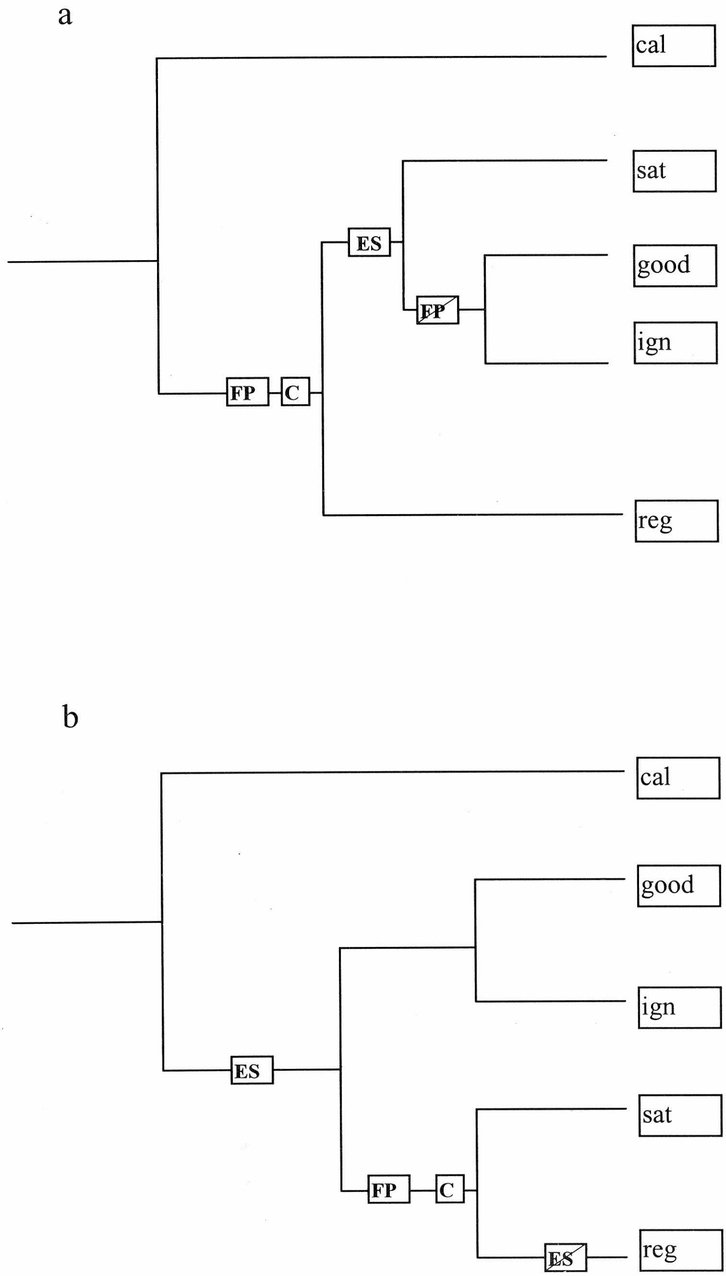

Fig. 17: Cladograms to illustrate two hypotheses on relationships within the genus *Regulus* (see text). - FP: final part of territorial song, ES: eyestripe, C: C-element-syntax; diagonal line: character reduced. - cal: *R. calendula*, good: *R. goodfellowi*, ign: *R. ignicapillus*, reg: *R. regulus*, sat: *R. satrapa*.

considered a symplesiomorphy of this group. It gives no information about the relationship between *R. regulus* and *R. satrapa*. Furthermore, C elements have not been retained by all *R. regulus* forms. The uncertainty of this hypothesis lies in the fact that at present it cannot be proven that the eyestripe originated only once, rather than having arisen a second time, independently and convergently, in *R. satrapa*.
Although distribution of the species in the eyestripe group is broad and disjunct (Europe, Taiwan, N America), close relationships among them have been postulated by a number of authors (HARTERT & STEINBACHER 1938, v.BOETTICHER 1941, GLUTZ v. BLOTZHEIM & BAUER 1991, ECK 1996), most vigorously by VOOUS (1962) who lumps all 3 species into one, *R. ignicapillus*, on the ground of morphological characters.

Hypothesis 2 (Fig. 17b): The eyestripe was acquired very early in *Regulus* evolution, and the final part of the bipartite song was added later. *R. ignicapillus* and *R. goodfellowi* are the sister group of *R. satrapa* and *R. regulus*. The latter group evolved the final part of the song and the C syntax, while *R. regulus* lost the eyestripe. This hypothesis presumes that the eyestripe firecrests (along with *R. calendula*) are the oldest species in the genus - an idea supported by their broad Palaearctic/Nearctic disjunction. Proto-*Regulus* branched away from this group relatively recently, and only then began to differentiate into the various subspecies. *R. ignicapillus* and *R. goodfellowi* never had bipartite songs; this song type was evolved by the predecessor of *R. regulus* and *R. satrapa*. This hypothesis cannot establish beyond doubt whether *R. regulus* and *R. satrapa* are indeed sister groups or whether *R. satrapa* evolved from *R. regulus* after the latter had differentiated a number of diverse forms (cf. UPGMA phenogram, Fig. 13). We tend towards the notion that *R. regulus* is a scion of the eyestripe group, which lost the eyestripe at the beginning of its radiation (cf. Fig. 16).
R. satrapa has been positioned near *R. regulus* by several authors (MAYR 1956 with reservations, DESFAYES 1965, MAYR & SHORT 1970, BECKER 1978, CRAMP 1992) on the basis of the auditory impression made by its song, and its bipartite verse was mentioned by MAYR (1956) and BECKER (1978)

Isolating mechanisms

The various verse types sung in Eurasia are understood to different degrees in the individual parts of the area. Our results confirm the finding of BECKER (1977a) that Goldcrests in Central Europe (subspec. *regulus*) give little or no response to territorial songs that lack a regular frequency alternation within the element groups of the main part. Not even the far eastern *japonensis* song (which does have regular frequency changes) elicited "good" responses in SW Germany (cf. Fig. 14, TS 6), and the responses to verses without frequency alternation were correspondingly slight. Within *japonensis* itself only moderate reactions were elicited when Hokkaido birds were tested with continental verses and conversely. From these results we infer that in the individual major populations considerable biologically relevant diversification of the songs has already taken place. Evidence is provided not only by syntax and element forms, but also by the responses to songs of other major populations. As yet, of course, we cannot say whether these differences suffice to obstruct gene flow upon secondary contact. THALER (1981) found that for "frictionless" mating, song must be accompanied by appropriate ethological characters and head patterning. It may be that *tristis*, presumably an especially long-isolated form, no longer meets these criteria.
Mention should be made here of the closely related tits *Parus rufonuchalis* and *P. rubidiventris*, the distributions of which are very similar to those of *R. r. tristis* (counterpart of *P. rufonuchalis*) and the *himalayensis* complex of *R. regulus* (counterpart of *P. rubidiventris*) (MARTENS 1975). These tits, which differ distinctly in size and song, today are partially sympatric; the Goldcrests have remained allopatric.

The song structures of the *R. regulus* subspecies have remained amazingly constant, for a long time, in their regions of the species' range. Throughout the Himalayan/Chinese region the main part of the song and some final parts are identical, despite the vast separation of populations on different mountain massifs. In the *japonensis* song individual final parts are the same on Hokkaido as in the Russian Far East, although the main part is considerably different. Within the continental area of *japonensis* certain final parts are identical in populations separated from one another by over 1000 km. Different subspecies living even further apart include the same motifs in the final part (*himalayensis* group and *japonensis*) or element groups in the main part (*japonensis*/*regulus*; *tristis*/final part of *japonensis*). We conclude that within a major population the songs are handed down with extraordinary precision, and that "cultural mutants" (JENKINS 1978) appear and can establish themselves only under certain conditions, presumably when a very small population is in a bottleneck situation. The Canaries (*teneriffae*) provide an example of such a situation, as does Hokkaido (*japonensis*). The Goldcrest thus offers an excellent opportunity to examine the differentiation of song structures in time and space. The recent subspecies have diverged sufficiently that in most cases the individual steps in differentiation are readily discernible. The hypothesis of KROODSMA et al. (1996) discussed above, postulating rapid change in the songs of the Oscines, can thus be refuted, at least for the Goldcrest.

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