Species limits in Northern Eurasian taxa of the common stonechats, *Saxicola torquatus* complex (Aves: Passeriformes, Muscicapidae)

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Abstract

The common stonechat *Saxicola torquatus* traditionally was considered as a polytypic species widely distributed in Africa, Europe and Asia. Recently, several authors have suggested that this formerly single species needs to be split into several distinct species composing the *Saxicola torquatus* complex based on mitochondrial markers. However, mitochondrial DNA alone is not sufficient for the evaluation of species status. In this paper, we reviewed the taxonomy of Northern Eurasian taxa from the complex based on morphometrics, plumage, song and alarm calls. The morphological and vocal data clearly matched the phylogroups reconstructed from mitochondrial DNA sequences, and separated Northern Eurasian taxa of the *Saxicola torquatus* complex into three groups: *rubicola*, *maurus* and *stejnegeri*. We proposed the species status for these three groups: European stonechat *Saxicola rubicola*, eastern stonechat *Saxicola maurus* and Japanese stonechat *Saxicola stejnegeri*. Among them, *S. stejnegeri* is a cryptic species as it cannot be distinguished by morphometrics and by worn spring plumage from *S. maurus*, but differs noticeably by male song.

Key words

Common stonechat, *Saxicola torquatus* complex, geographic variation, cryptic species, song divergence.

Introduction

In the last decades, it was revealed that many bird species actually are not a single species but rather complexes of several species, which are similar in morphology, but distinct in behavior, ecology, physiology etc (Bickford *et al*., 2006; Pfenninger & Schwenk, 2007). It is especially true for South Asia thanks to many recent advances in the taxonomy of Sino-Himalayan and Southeast Asian birds (Johansson *et al*., 2007; Martens *et al*., 2011; Päckert *et al*., 2012; Alström *et al*., 2013).

At same time, the revaluation of cryptic species in Northern Asia had received insufficient attention. Several recent studies however reveal large genetic and/or bioacoustic and/or morphological differentiation between western and eastern population groups of a species across Northern Eurasia. In several cases it was found that a taxon that was treated as a single species with discontinuous distribution in Northern Asia would in fact better be classified as two distinct species: white stork *Ciconia ciconia* – oriental stork *C. boyciana* (Archibald & Schmitt, 1991; Pavlova & Panov, 2005), and azure-winged magpie (*Cyanopica cyanus*) – Iberian magpie (*C. cooki*) (Fok *et al*., 2002; Kryukov *et al*., 2004; Zhang *et al*., 2012). In several other examples newly evaluated species lack an apparent distributional gap: red-breasted flycatcher *Ficedula parva* – taiga flycatcher *F. albicilla* (Svensson *et al*., 2005), western marsh harrier *Circus aeruginosus* –

eastern marsh harrier *C. spilonotus* (FEFELOV, 2001), great grey shrike *Lanius excubitor* – northern grey shrike (*Lanius borealis*) (OLSSON *et al*., 2010; TAJKOVA & RED'KIN, 2014), common buzzard *Buteo buteo* – eastern buzzard *B. japonicus* (KRUCKENHAUSER *et al*., 2004), great tit *Parus major* – Japanese tit *Parus minor* (KVIST *et al*., 2003; PÄCKERT *et al*., 2005), western yellow wagtail *Motacilla flava* – eastern yellow wagtail *M. tschutschensis* (PAVLOVA *et al*., 2003), and arctic warbler *Ph. borealis* – Kamchatka leaf warbler *Ph. examinandus* (SAITOH *et al*., 2010; ALSTRÖM *et al*., 2011; but the taxonomy is still debated: RED'KIN, 2013; RED'KIN *et al*., 2016).

More or less deep east-west divergence in Northern Eurasia was also found between different subspecies of a species. Examples include marsh tit *Poecile palustris* (TRITSCH *et al*., 2017), coal tit *Periparus ater* (PENTZOLD *et al*., 2013), goldcrest *Regulus regulus* (PÄCKERT *et al*., 2003), Eurasian nuthatch *Sitta europaea* (ZINK *et al*., 2006), barn swallow (SCORDATO & SAFRAN, 2014), black-tailed godwit *Limosa limosa* (HÖGLUND *et al*., 2009), great spotted woodpecker (ZINK *et al*., 2002), winter wren *Troglodytes troglodytes* (DROVETSKI *et al*., 2004), and several corvids (HARING *et al*., 2007). The willow tit *Poecile montanus* differs from the aforementioned examples because it does not display a continental east-west split (PAVLOVA *et al*., 2006; TRITSCH *et al*., 2017).

The most plausible interpretations for east–west divergence within a species and/or a species group in Northern Eurasia would be a wide distribution before the Pleistocene followed by the geographic isolation because of climatic changes during the ice age (HEWITT, 2000, 2004; SCHMITT, 2007). The exact evolutionary scenario could differ across species and species complexes (ZINK *et al*., 2008). Other theories, e. g. emergence of east-west divides from speciation by distance in a circular overlap (IRWIN *et al*., 2005) have received cautious but steady criticism (PÄCKERT *et al*., 2005; MARTENS & PÄCKERT, 2007; KOVYLOV *et al*., 2012; ALCAIDE *et al*., 2014).

The majority of the aforementioned studies analyzed mitochondrial DNA (mtDNA) and/or though rarely nuclear DNA. The taxonomic implications from mitochondrial DNA studies are somewhat limited, because several authors have concluded that mtDNA alone is not sufficient for the evaluation of species status (EDWARDS *et al*., 2005; TOBIAS *et al*., 2010). The species diversity of Northern Eurasian birds could be thus underestimated. The plausible solution is to use integrative taxonomy that takes into account also nuclear genetic markers, morphology, vocalization, ecology and behavior (PADIAL *et al*., 2010). Integrative taxonomy is especially helpful in the evaluation of cryptic species. Studies on the magpie *Pica pica* for example, have shown a clear east-west divergence in the Northern Palearctic based on DNA analysis (KRYUKOV *et al*., 2004; ZHANG *et al*., 2012; SONG *et al*., 2018). It was also found that bioacoustic data based on chatter call reflect DNA lineages. Taking together, these results allowed splitting Northern Eurasian magpies into the two taxa: *Pica pica* and *P. serica* (KRYUKOV *et al*., 2017).

The common stonechat *Saxicola torquatus* traditionally was considered as a single species with many subspecies widely distributed in Europe, Asia and Africa (ROBERTSON, 1977; CRAMP, 1988; ECK, 1996). In a view of some recent taxonomic advances, based on mtDNA sequence information this formerly single species needs to be split into several distinct species composing the *Saxicola torquatus* complex (WITTMAN *et al*., 1995; WINK *et al*., 2002; ILLERA *et al*., 2008; ZINK *et al*., 2009). However, as was mentioned above, mitochondrial markers alone are not sufficient for the evaluation of species status. Therefore, the taxonomy is still debated (URQUHART, 2002; CLEMENT & ROSE, 2015; DEL HOYO & COLLAR, 2016). Moreover, two currently accepted species (DEL HOYO & COLLAR, 2016) were nested within the *Saxicola torquatus* complex in mitochondrial DNA study(-ies): Fuerteventura stonechat *S. dacotiae* (ILLERA *et al*., 2008; ZINK *et al*., 2009) from the Canary Islands, and Reunion stonechat S. *tectes* from Reunion Island (ZINK *et al*., 2009).

Seven taxa from the *Saxicola torquatus* complex breed in Eurasia (Fig. 1): *rubicola* and *hibernans* in Europe, *stejnegeri* in the eastern Palearctic, *maurus* in the central Palearctic, *variegatus* and *armenicus* in the Caucasus and adjacent areas, and *indicus* and *przewalskii* in the Himalayas and adjacent China. Other names (e. g. *hemprichii*) should be in synonymy. In our opinion, the name "*S. m. hemprichii* EHRENBERG, 1833" was mistakenly applied by SVENSSON *et al*., (2012) to the west Caspian populations. Actually, *hemprichii* is in the synonymy of *variegatus*, the latter having priority. The reason is as follows. According to SVENSSON *et al*., (2012), a large mountain subspecies was firstly described under the name "*Parus variegatus* S. G. GMELIN, 1774" (terra typica – Shamakhi, east of Azerbaijan). Later, according to SVENSSON *et al*., (2012), this large subspecies was renamed as "*Saxicola torquatus armenica* STEGMANN, 1935". If the point of view of SVENSSON *et al*., (2012) was correct, West Caspian populations had to be named *S. m. hemprichii*, and populations from the mountains of Iran, Turkey and the Transcaucasia had to be named *S. m. variegatus*. However, the point of view of SVENSSON *et al*., (2012) based (1) on the mistake of STEGMANN (1935) who incorrectly placed the breeding specimen from Shamakhi in "*armenica*", and (2) on the incorrect interpretation of the characters of "*Parus variegatus* S. G. GMELIN, 1774", represented on the image in the original description. Actually, (1) the breeding area of "*armenica*" does not reaches East Transcaucasia including Shamakhi and (2) the coloration of specimen depicted in the original description of "*variegatus*" clearly fitted the variability limits of West Caspian populations (own data). That is why we place *S. m. hemprichii* in the synonymy of *S. m. variegatus*. Besides, the Sicilian population was given the name *archimedes* (CLANCEY, 1949). However, it remains questionable, whether the Sicilian birds are confirmed as a separate race, or *archimedes* should be in synonymy with *rubicola* (CORSO, 2001).

Recently it was found that *rubicola* (including *hibernans*), *maurus* (including *variegatus*) and *stejnegeri*
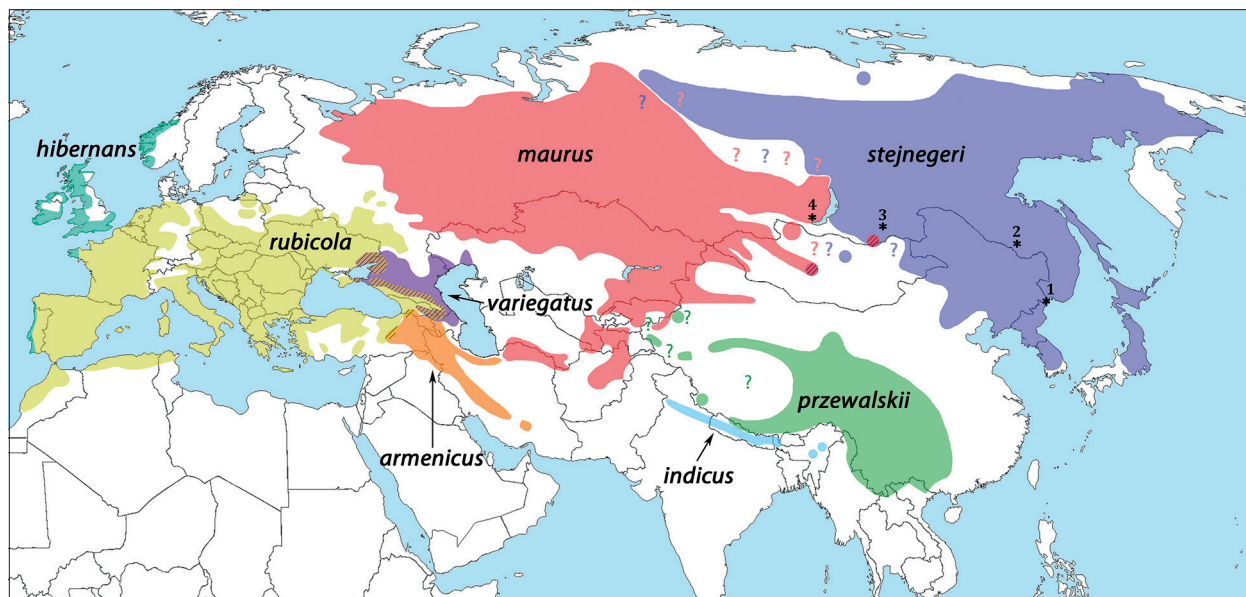
Fig. 1. Breeding ranges of the Eurasian taxa of the *Saxicola torquatus* complex. The hatched areas indicate zones of sympatry or possible sympatry. Numbers indicate the points of field work in Russian Federation: **1** – Khasan, Primorsky Kray, **2** – Khingan State Nature Reserve, Amur Oblast, **3** – Ivano-Arachleisk Nature Park, Chita Oblast, **4** – Irkutsk, Irkutsk Oblast.

could be classified as separate species based on the variation of mitochondrial ND2 gene sequences. It was also shown that *stejnegeri*, although very similar in appearance, had separated from *rubicola-maurus* well before differentiation occurred among the latter two taxa (ZINK *et al*., 2009). However, in the study by ZINK *et al*., (2009), haplotypes from the central Siberian clade (*maurus*) were found in a sample from Rostov-na-Donu area, just east of the Sea of Azov, in Russian Federation, and haplotypes from the east Siberian clade (*stejnegeri*) in a sample from Astrakhan, west of the Caspian Sea. Both findings may suggest that any firm conclusions about the phylogenetic relationships of *maurus* and *stejnegeri* are premature.

In this paper we analyzed morphometrics, plumage, song and alarm calls from throughout the range of three Northern Eurasian taxa of the *Saxicola torquatus* complex: *rubicola*, *maurus* and *stejnegeri*. We proposed that *S. rubicola*, *S. maurus* and *S. stejnegeri* could be recognized as separate species. We also shortly discussed the phylogenetic relationships of these taxa.

Materials and Methods

Field work

The two taxa (*maurus* and *stejnegeri*) were studied in the field (Fig. 1, Table S2–S3). Observations and sound recordings were carried out in the following locations: (1) *stejnegeri*: near Khasan, Primorsky Kray, Russian Federation in June 2016 by E.K., (2) *stejnegeri*: in Khingan State Nature Reserve, Amur Oblast, Russian Federation

in May–June 2013 by A.O. and M.G., (3) *stejnegeri*: in Ivano-Arachleisk Nature Park, Chita Oblast, Russian Federation in June–July 2015 by E.K., and (4) *maurus*: near Irkutsk, Irkutsk Oblast, Russian Federation in May–June 2015 by E.K.

Morphology

We measured and described the plumage of adult males and females of most specimens of three taxa of the *Saxicola torquatus* complex in several Russian collections (listed in Table S1). We described plumage under daylight condition using Naturalist's Color Guide (SMITHE, 1975). In the morphometry analysis, we used male specimens only. We measured the specimens of *rubicola* ($n = 14$), *maurus* ($n = 73$) and *stejnegeri* ($n = 63$) from throughout their ranges (Table S1). Measurements taken and used in the analysis were (in mm): (1) wing length (flattened and stretched), (2) tail length (measured from the base of central rectrices), (3) tarsus length, (4) bill length from skull to distal nares, (5) maximum bill depth, (6) bill width from bill base, (7) distance between wing tip and the tip of 2nd primaries, and (8) length of primaries projection.

Song

Recordings of 57 individuals of *rubicola* ($n = 10$), *maurus* ($n = 20$) and *stejnegeri* ($n = 27$), comprising 567 song strophes, were analyzed (Table S2). Most of the recordings were made by the authors (A.O. and E.K.). Additionally, we used song and calls (see below) recordings either taken from B. N. Veprintsev's collection of animal voices (Severtsov Institute of Ecology and Evolution of

Russian Academy of Sciences, Moscow, Russian Federation) or downloaded from Xeno-canto (www.xeno-canto.org). Besides, Alexander Rubtsov (Darwin State Museum, Moscow, Russian Federation) kindly provided recordings of two *maurus* males. Sonograms were produced and analyzed using Syrinx PC v. 2.6 (John Burt, www.syrinxpc.com) with an FFT size = 256, and a window type = Hanning.

Territorial song of each stonechat male consists of song strophes. Each song strophe consists of a number of syllables (Fig. S1, *a*). We define a syllable as either continuous line on a sonogram (i. e. element) or a combination of two or more elements separated by the pauses less than 10 ms or by a rapid alternation in frequency. Two or more elements in a syllable could be either different or similar. We thus introduced the term 'trill' that is the syllable consisted of several identical elements (Fig. S1, *a*). We chose 10 ms cut-off point because the distribution of pauses between elements was clearly bimodal, with most pauses either less than 10 ms (i. e. intra-syllable pauses) or more than 10 ms (between-syllable pauses) (Fig. S1, *b*).

In most cases we analyzed 10 consecutive song strophes per individual (mean 9.9).

(1) Duration of strophe, (2) number of syllables, (3) number of syllable types, (4) median syllable length, (5) median between-syllable pause, (6) minimum frequency, (7) maximum frequency, and (8) median frequency range of a syllable were measured for each song strophe or calculated based on the measurements of each syllable in the strophe. Median values of all strophes of an individual were calculated and used in the analysis.

Alarm call

All species on the approach of nest predators give two types of alarm calls, whit and chack (JOHNSON, 1971; GREIG-SMITH, 1980). They are commonly given in mixed sequences, although both occur singly. Using one-way ANOVA we found that males and female did not differ in time and frequency parameters of whits and chacks in the two taxa for which we had enough data (*rubicola*: $F = 3.03$, $p = 0.07$, 9 males and 6 females; *stejnegeri*: $F = 2.38$, $p = 0.08$, 10 males and 11 females). These findings were in accordance with the fact, that in bird species that have particular calls used by both sexes, there are minimal or no sex differences in those shared calls (VICARIO *et al*., 2001). Therefore, in the analysis the data were pooled across both sexes, and individuals of unknown sex were added.

For the alarm call analysis we used recordings of 53 individuals, belonging to three taxa of the *Saxicola torquatus* complex: *rubicola* ($n = 16$), *maurus* ($n = 15$) and *stejnegeri* ($n = 22$) (Table S3). All recordings had both whits and chacks. Usually we analyzed 10 whits and 10 chacks per individual (mean 9.9, for both alarm call types). (1) Duration, (2) minimum frequency, (3) maximum frequency and (4) frequency range were measured for each whit call. We measured duration only for each

chack call. Median values of measurements of both types of alarm calls of an individual were calculated and used in the analysis.

Statistical analysis

The analysis was performed in Statsoft Statistica 6.0 (STATSOFT INC [Internet] 2001) and in R 3.3.2 (R CORE TEAM, 2016). We analyzed morphometrics, song and two types of alarm calls separately.

Firstly, we used linear discriminant analysis (LDA) in the 'MASS' package in R (RIPLEY *et al*., 2017). LDA classify a given sample of predictors with highest posterior probability using Bayes' rule and tries to find a linear combination of predictors that gives maximum separation between the centers of the data. We then ran a principal component analysis (PCA) in Statistica 6.0. Bonferroni-adjusted two-sample Student t-tests were used to test differences between groups.

Results

Morphometrics

With respect to the morphometrics, the LDA of *rubicola*, *maurus*, and *stejnegeri* males resulted in 90.0% correct classification of these three groups (Wilks' $\lambda = 0.108$, $F = 13.44$, $n = 150$ males). The majority (11 out of 15) of misclassification cases were *maurus* males that were predicted to belong to *stejnegeri* (5 males), and vice versa (6 males).

The first three principal components had eigenvalues greater than one and PC1 explained 30.0% of the total variation. PC2 explained a cumulative 50.0% and PC3 a cumulative 63.8% of the total variation. Parameters of body size showed the highest absolute correlation with Factor 1: wing length, tail length and distance between wing tip and the tip of 2nd primaries. By contrast, bill size showed the strongest correlation with Factor 2: bill width and bill height. PC1 vs. PC2 showed individual measurements clustering according to the taxa (Fig. 2, *a*).

Among the three species, *rubicola* is characterized by comparatively short wing and tail, and had thus comparatively small body size (Table 1). The bill of *rubicola* is somewhat longer than that of both *maurus* and *stejnegeri*. By contrast, *stejnegeri* had relatively wide and deep bill.

It seemed impossible, however, to distinguish between these three taxa based on morphometrics only, because the measurements overlapped broadly (Table 1).

Plumage

The three taxa from the *Saxicola torquatus* complex could be distinguished based on the color of the fringes of the

Table 1. Univariate statistics for measurements of the males of three taxa of the *Saxicola torquta* complex. The values given are means ± SE, and min – max given in parentheses. Significance levels (Student t-test): **$p < 0.006$ (Bonferroni-adjusted p value); *$p < 0.01$; all others not significant.

|	*S. r. rubicola* (*n* = 14)	*S. m. maurus* (*n* = 73)	*S. (m.) stejnegeri* (*n* = 63)	*S. r. rubicola* versus *S. m. maurus*	*S. r. rubicola* versus *S. (m.) stejnegeri*	*S. m. maurus* versus *S. (m.) stejnegeri*
Wing lengt (mm)	65.3 ± 1.2 (59.0 − 68.0)	68.9 ± 1.7 (63.5 − 73.0)	68.0 ± 1.8 (63.0 − 72.0)	*	*	*
Tail length (mm)	45.5 ± 1.5 (42.5 − 48.0)	47.5 ± 2.1 (43.0 − 52.9)	48.0 ± 2.0 (42.0 − 52.7)	*	*	
Tarsus length (mm)	21.7 ± 0.7 (20.5 − 23.2)	20.9 ± 0.7 (18.5 − 23.0)	21.0 ± 0.7 (19.0 − 22.6)	*	*	
Bill length (mm)	7.9 ± 0.3 (7.4 − 8.7)	7.4 ± 0.4 (6.4 − 8.4)	7.6 ± 0.4 (6.4 − 8.6)	*	*	*
Bill depth (mm)	3.6 ± 0.2 (3.3 − 4.3)	3.7 ± 0.2 (3.2 − 4.4)	3.9 ± 0.2 (3.3 − 4.4)		*	*
Bill width (mm)	6.7 ± 0.4 (5.7 − 7.3)	6.5 ± 0.3 (5.5 − 7.2)	7.2 ± 0.3 (6.2 − 8.0)	**	*	*
Distance between wing tip and 2nd primaries (mm)	14.6 ± 1.3 (12.3 − 17.5)	15.5 ± 1.2 (12.1 − 18.7)	15.5 ± 1.3 (11.7 − 18.1)	*	*	
Primaries projection (mm)	5.4 ± 0.7 (3.7 − 6.5)	6.0 ± 1.1 (3.3 − 11.0)	5.4 ± 1.0 (2.8 − 8.3)	**		*
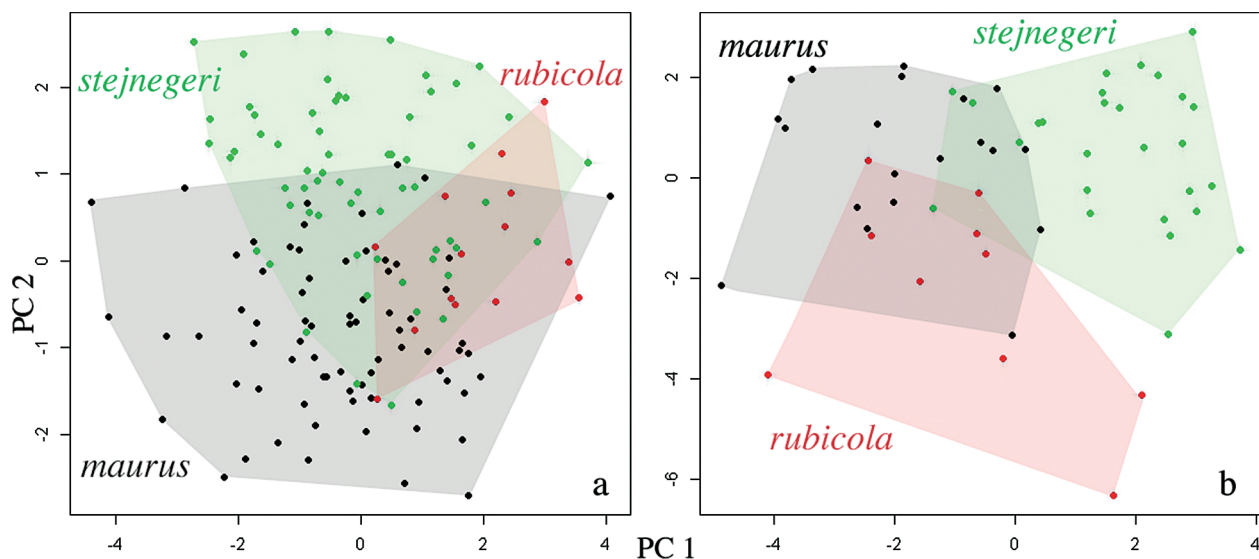
Fig. 2. PCA of eight external measurements of whole skin specimens (**a**) and PCA of eight acoustic parameters of song strophes (**b**) of males of three taxa of the *Saxicola torquatus* complex.

feathers of upperparts in fresh autumn plumage (Fig. 3), and on the amount of white on the sides of the neck, on the inner upperwing and on the rump in worm spring plumage.

In worn spring plumage the male of *rubicola* is distinguishable from the male of the two other taxa by its comparatively small patches of white on the sides of the neck, on the inner upperwing and on the rump. There are prominent darkish centers of the feathers on the uppertail coverts, which appear as dark longitudinal streaks. The rectrices are completely black showing no white at their base. The adult male in fresh autumn plumage is somewhat duller than in spring (fringes of the feathers of the upperparts − Mikado Brown C. 121C, according

to SMITHE, 1975) and has chestnut (Raw Sienna C. 136) fringes of the uppertail coverts. The female of *rubicola* is readily distinguishable by its darkish olive-brown upperparts and head, both having broad black stripes. It is due to broad white tips on the underwing coverts, that both sexes have whitish underwing.

The male of *maurus* in worn spring plumage is distinguishable by its broad patches of white on the sides of the neck, on the inner upperwing and on the rump. The rectrices have a white base in the majority of *maurus* individuals. The underwing is blackish and much darker than that of *rubicola*. In fresh autumn plumage the male of *maurus* has ochreous fringes (Ground Cinnamon C. 239) of the feathers of the upperparts. The feathers of the rump

Fig. 3. Dorsal and lateral views of males of *rubicola*, *maurus* and *stejnegeri* in worn spring plumage (*a*, *b*) and fresh autumn plumage (*c*).

Table 2. Univariate statistics for measurements of the song strophes of the males of three taxa of the *Saxicola torquta* complex. The values given are means ± SE, and min – max given in parentheses. Significance levels (Student t-test): **$p < 0.006$ (Bonferroni-adjusted p value); *$p < 0.01$; all others not significant.

	S. r. rubicola (*n* = 10)	*S. m. maurus* (*n* = 20)	*S. (m.) stejnegeri* (*n* = 27)	*S. r. rubicola* versus *S. m. maurus*	*S. r. rubicola* versus *S. (m.) stejnegeri*	*S. m. maurus* versus *S. (m.) stejnegeri*
Duration of strophe (s)	1.36±0.10 (1.23−1.53)	1.34±0.25 (1.13−2.11)	1.01±0.21 (0.73−1.49)		**	**
Number of syllables	13.0±2.6 (8.5−16.5)	15.8±3.7 (11.0−26.0)	10.5±2.2 (7.0−15.0)			**
Number of syllable types	12.1±2.3 (8.5−15.0)	13.8±2.8 (10.5−22.5)	9.8±2.1 (6.0−14.5)			**
Median syllable length (s)	0.07±0.02 (0.05−0.10)	0.05±0.01 (0.04−0.07)	0.07±0.01 (0.05−0.10)	*		**
Median between-syllable pause (s)	0.03±0.01 (0.01−0.04)	0.02±0.01 (0.008−0.03)	0.02±0.01 (0.008−0.03)			
Minimum frequency of a strophe (kHz)	2.3±0.2 (2.1−2.7)	2.3±0.4 (1.4−2.8)	2.4±0.2 (2.0−2.8)			
Maximum frequency of a strophe (kHz)	7.5±0.4 (7.0−8.1)	7.3±0.3 (6.9−7.9)	6.4±0.3 (5.8−6.9)		**	**
Median frequency range of a syllable (kHz)	2.2±0.2 (1.7−2.9)	2.0±0.3 (1.2−4.1)	1.4±0.2 (1.0−2.2)		**	**

and the uppertail coverts have pale sandy (Cinnamon C. 39) or rusty-brown (Antique Brown C. 37) fringes. Compared to female *rubicola*, the *maurus* female shows upperparts having the more expressed black streaks.

We have detected no stable differences in worn plumage between *maurus* and *stejnegeri*. We have found however only some weak differences in worn plumage between these two taxa, but these are evident only in a series of individuals and thus were not useful for species distinction. There was a little less white on the sides of the neck, on the inner upperwing, on the rump and on the base of rectrices in males of *stejnegeri*. Compared to female *maurus*, the females of *stejnegeri* have little more dark upperparts, which somewhat obscured black streaks.

The prominent differences between *maurus* and *stejnegeri* appear in fresh autumn plumage only. It is the color of the fringes of the feathers of the rump and the uppertail, that is useful for identification (Fig. 3): *stejnegeri* has chestnut-red fringes (Amber C. 36) and *maurus* has much more pale sandy (Cinnamon C. 39) or rusty-brown fringes (Antique Brown C. 37). Besides, *stejnegeri* has chesnut (Raw Sienna C. 136) fringes of the feathers of the upperparts that appear darker than that of *maurus*.

Song

The songs of *maurus*, *rubicola* and *stejnegeri* were generally similar. Each song strophe lasted 1−1.5 sec and built up of 10−20 short syllables interspersed with one or several single-element trill(s) (Fig. 4). The trills were very characteristic for the songs of *maurus* and *rubicola*, but were more rarely observed in *stejnegeri*. Because of a rarity of trills, singing of *stejnegeri* audibly seemed to be more melodious.

The LDA of songs in *maurus*, *rubicola* and *stejnegeri* males resulted in 86.0% correct classification of these three groups (Wilks' λ = 0.090, F = 13.67, *n* = 57 males). The majority (5 out of 8) of misclassification cases were *rubicola* males that were predicted to belong to *maurus*. In addition to the misclassified ones above, there were also two *maurus* predicted to belong to *rubicola* and one *stejnegeri* predicted to belong to *rubicola*.

The first three principal components had eigenvalues greater than one. PC1 explained 45.1% of the total variation; PC2 explained a cumulative 68.1% and PC3 a cumulative 81.2% of the total variation. The following parameters showed the highest absolute correlations with Factor 1: duration of strophe, number of syllables, number of syllable types, and maximum frequency. By contrast, both median syllable length and median between-syllable pause showed the strongest correlation with Factor 2. PC1 vs. PC2 showed individual measurements clustering according to the taxa (Fig. 2, *b*).

Therefore, the LDA and PCA analysis clearly separated *stejnegeri* from both *maurus* and *rubicola*, which were closer to each other. Moreover, it was impossible to separate songs of *maurus* and *rubicola* in several cases. Song strophes of *stejnegeri* were the shortest, and had the lowest maximum frequency and the narrowest frequency range (Table 2).

Alarm call

All species on the approach of nest predators give two types of alarm calls, whit and chack. Whits are often modulated notes with energy limited to a narrow frequency range. Chacks are usually shorter than whits, and cover a much wider frequency range. Both whits and
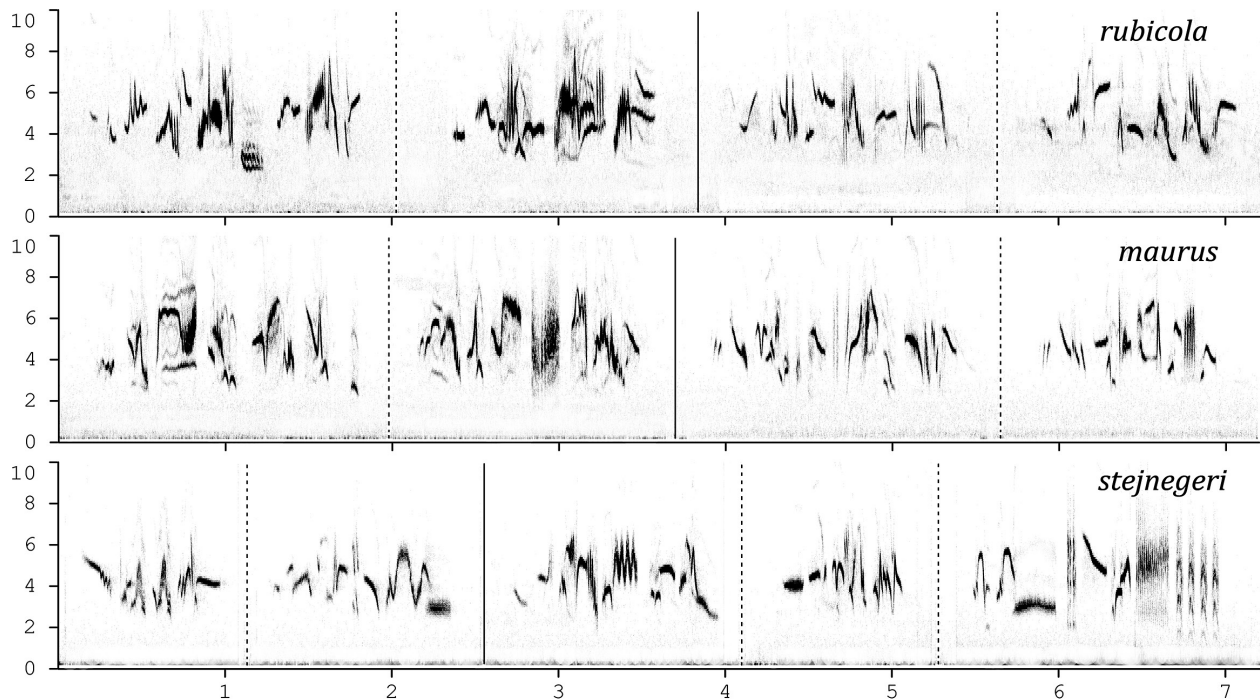
Fig. 4. Spectrograms of song strophes of three taxa of the *Saxicola torquatus* complex (x-axis = time in seconds; y-axis = frequency in kHz). Strophes separated by dotted lines are from the same male. All others are from different males.
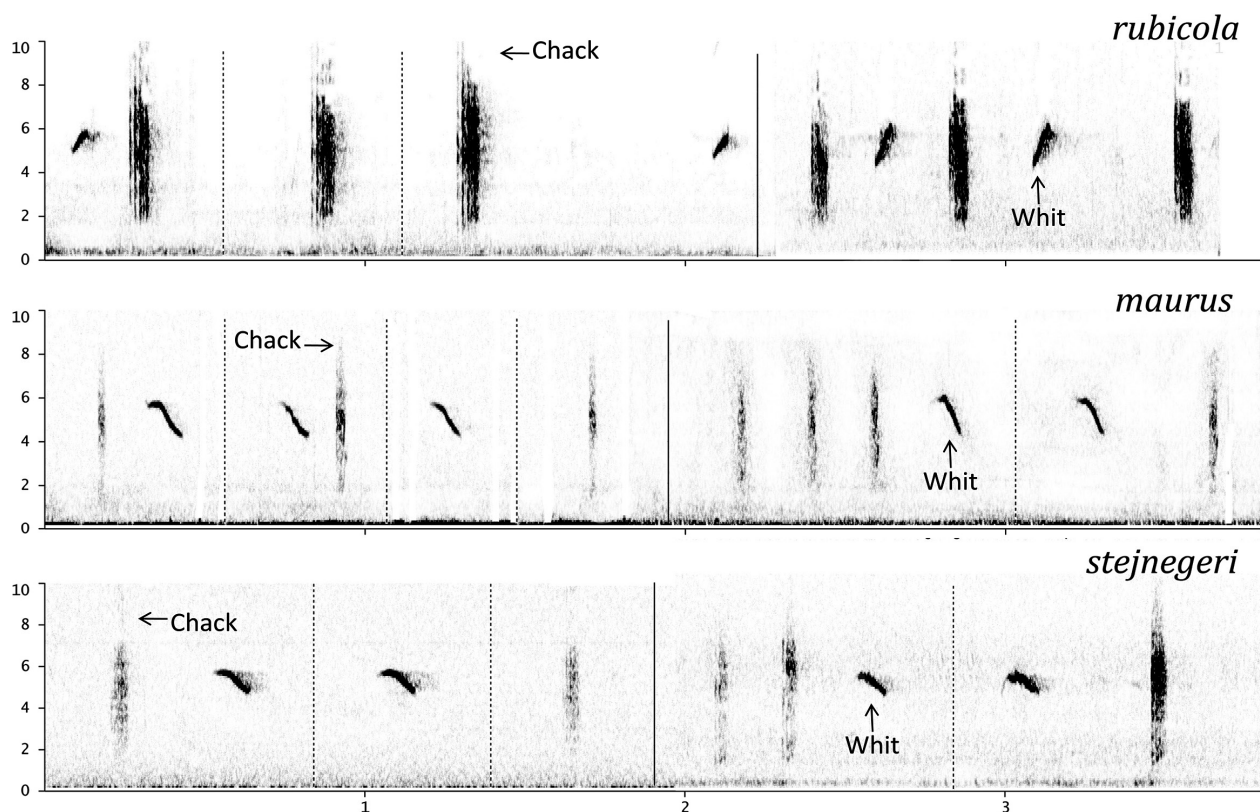

Fig. 5. Spectrograms of two types of alarm calls (Whits and Chacks) in three taxa of the *Saxicola torquatus* complex (x-axis = time in seconds; y-axis = frequency in kHz). Calls separated by dotted lines are from the same individual. All others are from different individuals.

chacks are generally similar in all species analyzed, although differed in detail (Fig. 5).

The LDA of whits in *maurus*, *rubicola* and *stejnewgeri* individuals resulted in 94.3% correct classification

(Wilks' λ = 0.111, F = 23.37, n = 53 individuals). The first two principal components had eigenvalues greater than one. PC1 explained 45.6%, and PC2 explained a cumulative 80.6% of the total variation. Frequency range and

Table 3. Univariate statistics for measurements of chack and whit calls of individuals of three taxa of the *Saxicola torquta* complex. The values given are means ± SE, and min−max given in parentheses. Significance levels (Student t-test): *$p < 0.01$ (Bonferroni-adjusted p value); all others not significant.

|	*S. r. rubicola* (n = 16)	*S. m. maurus* (n = 15)	*S. (m.) stejnegeri* (n = 22)	*S. r. rubicola* versus *S. m. maurus*	*S. r. rubicola* versus *S. (m.) stejnegeri*	*S. m. maurus* versus *S. (m.) stejnegeri*
Duration of chack (s)	0.06±0.01 (0.05−0.07)	0.04±0.01 (0.03−0.04)	0.06±0.01 (0.05−0.07)	*		*
Duration of whit (s)	0.06±0.01 (0.04−0.08)	0.10±0.01 (0.09−0.12)	0.09±0.01 (0.07−0.11)	*	*	*
Minimum frequency (kHz)	4.4±0.3 (3.7−4.7)	4.0±0.2 (3.7−4.5)	4.4±0.2 (3.7−4.7)	*		*
Maximum frequency (kHz)	6.1±0.2 (5.7−6.5)	5.9±0.2 (5.6−6.4)	5.6±0.2 (4.9−6.0)		*	*
Frequency range (kHz)	1.7±0.4 (1.1−2.5)	1.9±0.2 (1.5−2.1)	1.2±0.1 (1.0−1.5)		*	*
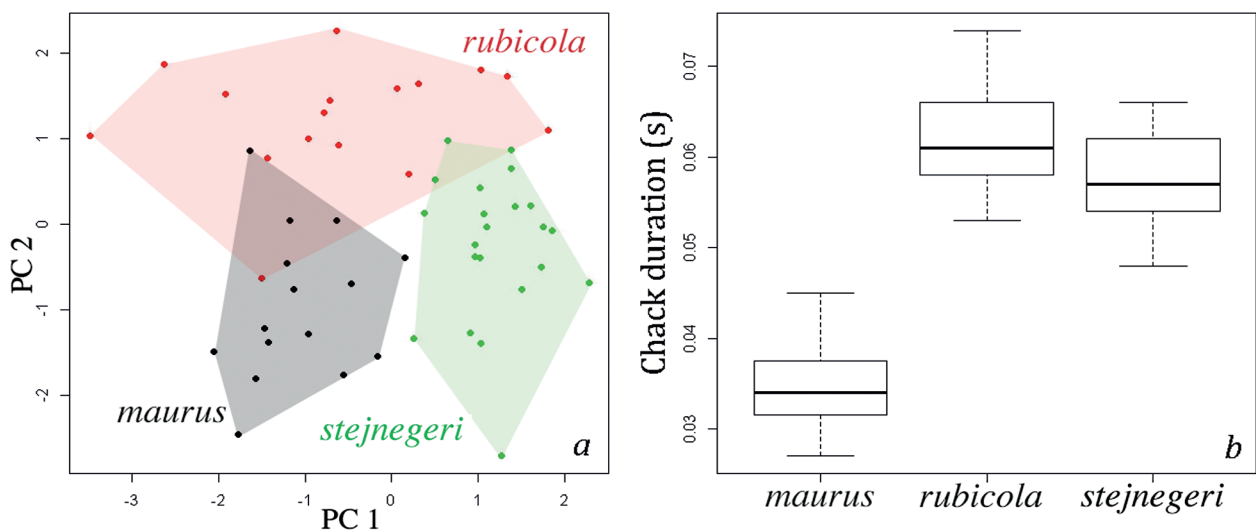
Fig. 6. PCA of four acoustic parameters of whit calls (*a*) and durations of chack calls (*b*) of three taxa of the *Saxicola torquatus* complex.

maximum frequency showed the highest absolute correlations with Factor 1, and whit's duration and minimum frequency showed the strongest correlation with Factor 2. Fig. 6, *a* shows the 'PC1 vs. PC2' scatterplot (see also Table 3).

Besides, we have found one more stable differences between the structure of whits of *rubicola* and that of the two other taxa. The shape of frequency modulation of whits of *rubicola* was always 'ascending' (frequency ascends from the begging to the end of a whit), while whits of the others had 'descending' modulation (Fig. 5).

The duration of chacks in *rubicola* and *stejnegeri* did not significantly differ one from another, but differed significantly from that of *maurus* (Fig. 6, *b*; Table 3).

Discussion

The morphological (both plumage and measurements) and vocal (both song and calls) data clearly matched the phylogroups reconstructed from mtDNA sequences

(ZINK *et al.*, 2009), and separated Northern Eurasian taxa of the *Saxicola torquatus* complex into the three groups: *rubicola*, *maurus* and *stejnegeri*. Besides, *variegatus* was thought to be a closely relative to *maurus* based on mitochondrial DNA study (ZINK *et al.*, 2009). The taxonomy of Southern Eurasian's *armenicus*, *indicus* and *przewalskii* remains to be studied.

With respect to vocalization, *maurus* and *rubicola* had the most similar songs, although they clearly differed in alarm calls. These two species also differed subtly, but noticeably, in external morphology. Our result confirmed previously published information concerning differences between the taxa in plumage and morphometrics (ROBERTSON, 1977; URQUHART, 2002; HELLSTRÖM & WÆRN, 2011). In worn spring plumage male of *rubicola* is distinguishable by its comparatively small patches of white on the sides of the neck, by pale (not blackish) underwing-coverts and by the prominent darkish centers of the feathers on the uppertail coverts, which appear as dark longitudinal streaks on the rump.

The two Asian taxa (*maurus* and *stejnegeri*) morphologically were the most similar. These two taxa cannot

be reliably distinguished by morphometrics and by worn spring plumage. The only feature useful for identification appears in fresh autumn plumage: the color of the fringes of the feathers of the rump and the uppertail. Besides, HELLSTRÖM & NOREVIK (2014) revealed the presence of dark spotting on the uppertail-covert of ca. 60% of birds in fresh autumn plumage, whereas *maurus* generally but not always (own data) shows unmarked rump. In contrast to morphology, song of *stejnegeri* was the most distinctive among the three taxa analyzed. Bioacoustic data are thus in agreement with mitochondrial lineages in so far as *stejnegeri* has apparently split from *maurus* and *rubicola* before differentiation occurred among the latter two taxa. *S. stejnegeri* thus appeared to be a cryptic species that is extremely similar in the suite of external characters to *maurus*, but differs in song and calls (this study) and mtDNA (ZINK *et al.*, 2009).

The zones of symparty between different taxa from the *Saxicola torquatus* complex in Eurasia are poorly known. The only exception is the sympatry zone between *rubicola* and *variegatus* in Rostov Oblast, Russian Federation (Fig. 1). Here, these two taxa bred in different although overlapping habitats without any signs of intergradations (KAZAKOV & BAKHTADZE, 1999; BAKHTADZE, 2002).

Little is known about the distributional ranges of *maurus* and *stejnegeri* in Transbaikalia, where a sympatry zone might exist. Although several authors stated a wide range of intergradation between *maurus* and *stejnegeri* in Siberia (CRAMP, 1988; HELLSTRÖM & WÆRN, 2011), this statement is apparently wrong (HELLSTRÖM & NOREVIK, 2014). Interestingly, stonechats are more or less absent (except on migration) from the area just south and east of Lake Baikal, including the delta of the Selenga River (FEFELOV *et al.*, 2001). Therefore, the transition from *maurus* to *stejnegeri* in southern Siberia may be abrupt. According to our analysis of museum collections, as well as on published data (ZINK *et al.*, 2009, 2010), there were only two points, where both taxa have been collected (Fig. 1). First point located near Chikoy urban-type settlement in the Republic of Buryatia, Russian Federation, where *stejnegeri* is the commonest stonechat, but several *maurus* specimens were collected during the breeding season (ZINK *et al.*, 2010). The second point located in the eastern part of the Khangai Mountains (Central Mongolia), where one specimen of *stejnegeri* was collected along with several specimens of *maurus*. In the second point, however, the specimen of *stejnegeri* was collected on 21.08.1926 (deposited in the collection of Zoological Institute of the Russian Academy of Sciences), and could be thus on migration. Therefore, new studies on distribution ranges of *maurus* and *stejnegeri* in Eastern Siberia and Mongolia are extremely needed.

What happens where *rubicola* and *armenicus* meet in Turkey is unclear (KIRWAN *et al.*, 2008). URQUHART (2002), however, stated that the two taxa show different habitat preferences in that region, with *armenicus* present in mountain habitats and *rubicola* in the lowlands. In the Himalayas, *przewalskii* was found to be parapatric with *indicus* being separated by elevation (MARTENS & ECK, 1995).

The comparative studies of breeding biology, ecology and behavior of Eurasian stonechats are almost completely absent. Recently, however, GOLOVINA & OPAEV (2016) reviewed some original and published data (FUJIMAKI & SHIBNEV, 1991; FUJIMAKI *et al.*, 1994) on the breeding biology and social organization of *stejnegeri*. Comparing biology and behavior of *stejnegeri*, with those of well-studied *rubicola* and *hibernans* (PARRINDER & PARRINDER, 1945; JOHNSON, 1971; FULLER & GLUE, 1977; GREIG-SMITH, 1979; URQUHART, 2002; BANIK, 2003) showed that most differences between them concern territory size and breeding density. *S. stejnegeri* usually had smaller territories and bred in higher densities, than both *rubicola* and *hibernans*. By contrast, habitat and breeding biology (e. g. nest and egg) appeared to be rather similar among the two taxa.

Summarizing, our study presented data that is valuable for the evaluation of the taxonomy of the *Saxicola torquatus* complex. Based on our and earlier genetic findings, we proposed the species status for the following three taxa:

1 European stonechat *Saxicola rubicola* (LINNAEUS, 1766), including *S. r. rubicola* and *S. r. hibernans*.

2 Eastern stonechat *Saxicola maurus* (PALLAS, 1773), including at least three subspecies: *S. m. maurus*, *S. m. variegatus* and *S. m. armenicus* (the taxonomic affinities of *indicus* and *przewalskii* that usually merge into *S. maurus* remain to be studied).

3 Japanese stonechat *Saxicola stejnegeri* (PARROT, 1908), monotypic.

Our song data are also in agreement with previous phylogenetic reconstructions, because we revealed that that the song of *S. stejnegeri* is the most distinct among the three taxa analyzed.

Acknowledgments

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File 1. Supplementary_Table_S1.pdf.

File 2. Supplementary_Table_S2.pdf.

File 3. Supplementary_Table_S3.pdf.

File 4. Supplementary_Fig_S1.pdf.