Geographical variation in Black Redstart *Phoenicurus ochruros* (S. G. Gmelin, 1774) calls

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Summary.—Black Redstart *Phoenicurus ochruros* occurs over a broad range from Western Europe and north-west Africa to Central Asia. Seven subspecies are usually recognised, which can be divided morphologically into a grey-and-white-bellied western group ('Western Black Redstart'; two subspecies) and an orange-bellied eastern group ('Eastern Black Redstart'; five subspecies). Because vocalisations might help to understand relationships between these taxa, we analysed the calls of six of the seven subspecies. We demonstrate that calls can be grouped into one of three geographical variants. One is formed by the western subspecies breeding in Europe, the morphologically intermediate subspecies *ochruros* and Eastern Black Redstarts from the Altai and Mongolia. Further south-east, birds call at lower frequencies on average and within a smaller frequency range (group 2). The third group is formed by the eastern subspecies *rufiventris* which differs from all other taxa, with a descending instead of a rising call, given at much lower frequencies.

Black Redstart *Phoenicurus ochruros* occupies a broad range from Portugal and North Africa in the south-west, southern Norway and Sweden in the north-west, to Mongolia and China in the east. Seven subspecies are usually recognised, which can be divided into the grey-and-white-bellied western forms *aterrimus* and *gibraltariensis* ('Western Black Redstart') and an orange-bellied eastern group (Collar 2021) containing the subspecies *ochruros*, *semirufus*, *phoenicuroides* (including *alexandrovi* and *murinus* as synonyms) and *rufiventris* (including *pleskei* and *xerophilus*) ('Eastern Black Redstart') (Cramp 1988, Glutz von Blotzheim 1988, Nicolai *et al*. 1996, Steijn 2005, Fedorenko 2018, Shirihai & Svensson 2018, Sangster 2021; Fig. 1). Despite striking plumage differences between males of the western and eastern subspecies groups all taxa are considered to belong to one species by the main taxonomic authorities (e.g., Dickinson & Christidis 2014, Collar 2021, Gill *et al*. 2021). One reason for this approach is that males of the nominate subspecies *ochruros*, which breeds in Turkey and the Caucasus, shows such a variable amount of orange on the belly that its plumage is considered intermediate between western and eastern subspecies groups. Based on mtDNA (analyses of cytochrome b), Sangster (2021) supported this taxonomic approach as there seems to be a lack of correspondence between clades and subspecies limits, at least from Turkey eastwards. Vocalisations form an additional character of potential insight for avian systemists (Alström & Raft 2003). Analyses of song and calls might therefore provide new information on relationships among Black Redstart subspecies. Martens & Eck (1995) compared songs of birds from Nepal (*rufiventris*), Iran (*ochruros* or *phoenicuroides*) and Germany (*gibraltariensis*), but obtained ambiguous results. To our knowledge, however, calls have yet to be analysed from a geographical perspective (*cf*. Constantine *et al*. 2021) and any subspecific differences are yet to be described. For this study, we therefore assembled recordings of calls from the entire breeding range of Black Redstart, including both western and all but one of the eastern subspecies. We examined

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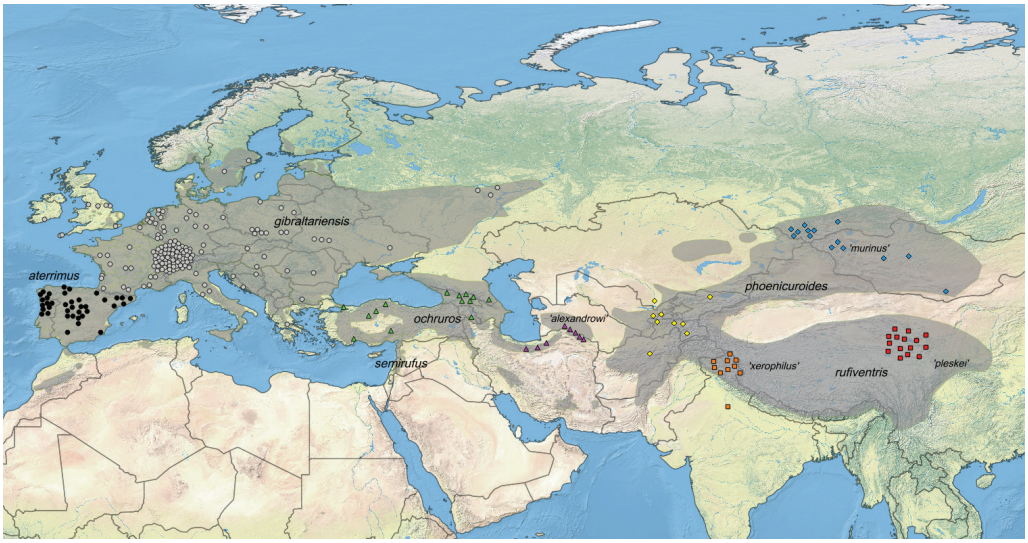

Figure 1. Recordings used herein (dots) and the breeding range of Black Redstart *Phoenicurus ochruros* subspecies, based mainly on BirdLife International and Handbook of the Birds of the World (2021) but adapted slightly based on Steijn (2005), Fedorenko (2018), Keller *et al.* (2020) and breeding records from www.ebird.com. Map: Natural Earth (www.naturalearthdata.com).

typical calls, generally used in contact or alarm and often described as a soft rising *vist*, which is frequently used in combination with a *tuc* call (Constantine *et al*. 2021).

Methods

We assembled sound-recordings of Black Redstart contact calls from 277 individual birds. Sources included www.xenocanto.org (n = 91 individuals, XC), our own or privately shared recordings (n = 72), www.macaulaylibrary.org (n = 38; ML), www.inaturalist.org (n = 20; iN), www.youtube.com (n = 18), www.observation.org and www.waarneming.nl (n = 10), B. N. Veprintsev Phonotheque of Animal Voices (n = 11, VPAV), The Sound Approach (n = 8, TSA), www.facebook.com (n = 5) and avocet.integrativebiology.natsci.msu.edu (n = 4). In places where different subspecies occur on migration or in winter, e.g., in India and Iran, only recordings made between mid March and mid September, or of obviously territorial birds were analysed (e.g., breeding, or if also singing). Only one recording was used if several recordings from the same location in the same year were available, unless it was proven that different individuals were involved and recordings available in several sources were used only once. A list of all recordings used can be found in the Supplementary Material. We listened to the calls and made sonograms. For this, all recordings were converted to 44 kHz .wav files (16 bit). Sonograms were prepared using Raven (K. Lisa Yang Center for Conservation Bioacoustics 2016). We used KaiserWindow to visualise calls in combination with a sample overlap of 95% and a DFT size of 700 samples. As a first step, we used sonograms to manually assess the min. and max. frequency for each individual. As each individual's calls were relatively uniform (Appendix 3), we chose one representative call per individual for testing. In a second step—serving as a quality control—we used a more observer-independent measurement via the software Audacity (Audacity Team 2021). On Audacity sonograms we calculated the lower and upper frequencies where the intensity was 20 db(A) lower relative to the peak amplitude of the same call (Appendix 1). Such a threshold below the peak minimises the influence of artefacts when measuring uncalibrated

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field recordings (Zollinger *et al*. 2012) and is less subject to personal interpretation when measuring frequencies. Results of both methods were compared, found to be highly correlated (Appendix 2), and produced very similar results (Appendix 4). Taking into account the aforementioned advantages, all data given in the Results and Discussion refer to lower and upper frequencies calculated using the –20 dB(A) threshold. To interpret effect size data, we calculated overlap coefficients according to Vijaymeena & Kavith (2016) based on outlines of the plotted data. An overlap coefficient of 1.0 means that the smaller of two samples falls completely within the larger sample. If the samples do not overlap at all, the coefficient equals 0.0. As there are two morphological groups (Western and Eastern), our null hypothesis was that *if* calls of the eastern and western groups differed, *ochruros*—with its intermediate plumage—would potentially possess intermediate calls as well.

Results

Calls of western subspecies.—In general the call of *gibraltariensis* (n = 161) and *aterrimus* (n = 43) can be described as *vist*. It is a short and thin rising whistle starting between 4.3 and 5.0 kHz (in 93% of all analysed birds the lower frequency is within this range) and ends mostly *c*.1 kHz higher, between 5.3 and 6.2 kHz (97%, Fig. 2). Measures overlapped strongly for the two subspecies (Fig. 3) and overlap coefficient was high (0.88) but many *aterrimus* gave calls at the lower end of the spectrum, resulting in slightly different mean values (Fig. 4, Tables 1–2). On the sonogram, some birds have a downward-inflicted 'hook' at the end of the call. This 'hook' is mostly very small, but occasionally reaches as low as the initial frequency, e.g., see birds 1, 5 and 6 in Fig. 2. Such a 'strong' hook is uncommon, and was observed in <10% of all *aterrimus* and *gibraltariensis*. In three recordings, all from Portugal, the downward part was even more prominent than the rising part.

Calls of ochruros.—*Contra* our null hypothesis, the calls of *ochruros* fall completely within the range of the western group (n = 17, including three from western Turkey where *gibraltariensis* and *ochruros* are believed to meet; Glutz von Blotzheim 1988; see Fig. 5). They sound identical to the ear, and all measurements overlap resulting in very high overlap

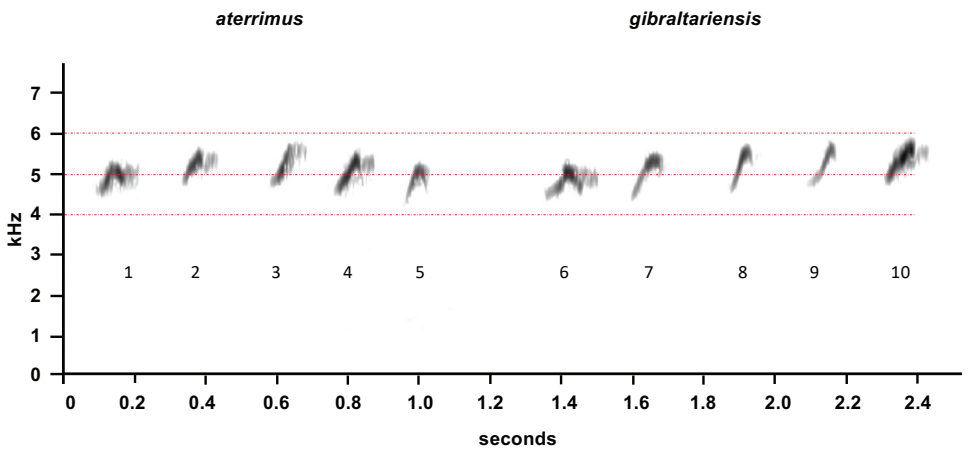

Figure 2. Variation in calls of *Phoenicurus ochruros aterrimus* (1–5) *and P. o. gibraltariensis* (6–10). 1: Spain, 5 June 2020 ('canogal14'; iN64353923), 2: Spain, 12 April 2020 (X. Riera; XC544651), 3: Spain, 22 March 2018 (E. Poveda; XC459359), 4: Spain, 29 March 2019 (P. Åberg; XC148957), 5: Portugal, 2 August 2021 (M. Ferreira; iN89677006), 6: Switzerland, 28 May 2017 (T. Lüthi; XC378169), 7: Sweden, 18 September 2019 (P. Kappel; XC497730), 8: England, 14 April 2021 (J. Spinks; XC638960), 9: European Russia, 20 April 2014 (A. Lastukhin; XC189174), 10: Belgium, 12 June 2020 (H. Matheve; XC567747).

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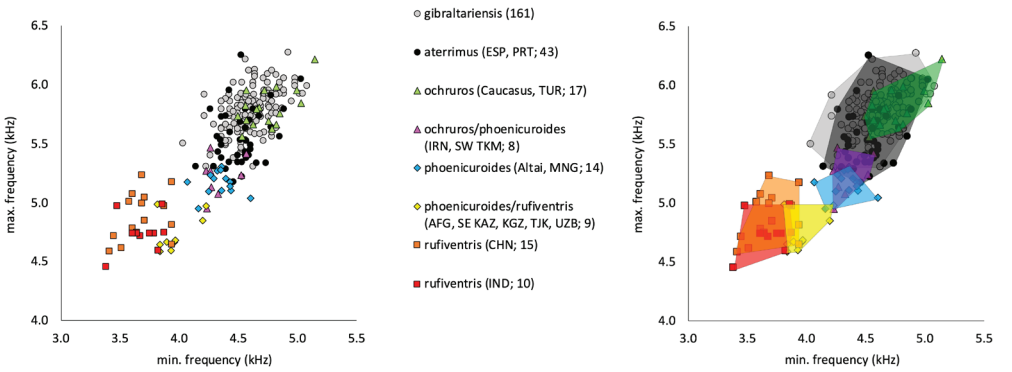

Figure 3. Plotted min. and max. frequencies for all analysed birds (including outlines on the left graph). Countries are indicated by their official ISO-3166 three-letter codes.

TABLE 1
Frequencies (mean ± standard deviation, range) for all analysed subspecies and supposed intergradation zones. Countries are indicated by their official ISO-3166 three-letter codes.

	Min. frequency (kHz)	**Max. frequency (kHz)**	**entire range (kHz)**	***n***
aterrimus (ESP, PRT)	4.523 ± 0.176 (4.138–5.025)	5.556 ± 0.231 (5.176–6.255)	1.033± 0.241 (0.607–1.733)	43
gibraltariensis	4.607 ± 0.180 (4.031–5.078)	5.789 ± 0.183 (5.307–6.274)	1.182 ± 0.187 (0.690–1.708)	161
ochruros (Caucasus, TUR)	4.738 ± 0.187 (4.494–5.143)	5.812 ± 0.164 (5.562–6.222)	1.074 ± 0.166 (0.819–1.388)	17
ochruros / *phoenicuroides* (N IRN, SW TKM)	4.332 ± 0.134 (4.227–4.566)	5.166 ± 0.172 (4.951–5.470)	0.899 ± 0.177 (0.722–1.210)	8
phoenicuroides (Altai, MNG)	4.334 ± 0.131 (4.064–4.602)	5.166 ± 0.099 (4.951–5.307)	0.832 ± 0.165 (0.442–1.112)	14
phoenicuroides / *rufiventris* (AFG, SE KAZ, KGZ, TJK, UZB)	3.960 ± 0.153 (3.811–4.227)	4.742 ± 0.155 (4.587–4.988)	0.782 ± 0.156 (0.654–1.177)	9
rufiventris (CHN, IND)	3.682 ± 0.165 (3.377–3.933)	4,831 ± 0.196 (4,456–5.235)	1.148 ± 0.216 (0.719–1.555)	25

coefficients (Table 2), although mean values are even slightly higher (and the highest of all taxa) compared to *gibraltariensis* and *aterrimus*.

Calls of eastern subspecies.—The calls of birds from the Altai and Mongolia (*phoenicuroides*) are generally similar in shape and sound to Western Black Redstarts. However, mean frequencies are much lower: on average the start is 0.3 kHz lower than in *gibraltariensis* (range 4.064–4.602 kHz) and the call ends around 0.5 kHz lower (4.951–5.307 kHz) (Fig. 6, Table 1) resulting in low overlap coefficients with the other eastern subspecies (Table 2). The entire range of the call is on average also reduced vs. western subspecies (Table 1). In northern Iran and neighbouring Turkmenistan, where the ranges of *ochruros* and *phoenicuroides* meet (Glutz von Blotzheim 1988), the calls are clearly lower and with a smaller range than in *ochruros* from further west (Table 1, Fig. 5), but on average still slightly higher than birds further east. To the human ear, calls from the Altai, Mongolia as well as northern Iran and neighbouring Turkmenistan are rather similar to western *vist* calls. Birds from Afghanistan, Tajikistan, south-east Kazakhstan, Kyrgyzstan and Uzbekistan (i.e., the southern range of *phoenicuroides*) have different calls with a very small ascending part, followed by a rather constant middle section, before ending in a descending part that

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TABLE 2
Overlap coefficients for all analysed subspecies and supposed intergradation zones. Colour codes range from dark blue (high overlap coefficient) to orange (no overlap).

	aterrimus	*gibraltariensis*	*ochruros*	*ochruros / phoenicuroides*	*phoenicuroides*	*phoenicuroides / rufiventris*	*rufiventris* (India)	*rufiventris* (China)
aterrimus		0.88	0.81	0.61	0.11	-	-	-
gibraltariensis	0.88		0.89	0.38	-	-	-	-
ochruros	0.81	0.89		-	-	-	-	-
ochruros / phoenicuroides	0.61	0.38	-		0.48	-	-	-
phoenicuroides	0.11	-	-	0.48		0.02	-	-
phoenicuroides / rufiventris	-	-	-	-	0.02		0.16	0.34
rufiventris (India)	-	-	-	-	-	0.16		0.75
rufiventris (China)	-	-	-	-	-	0.34	0.75	

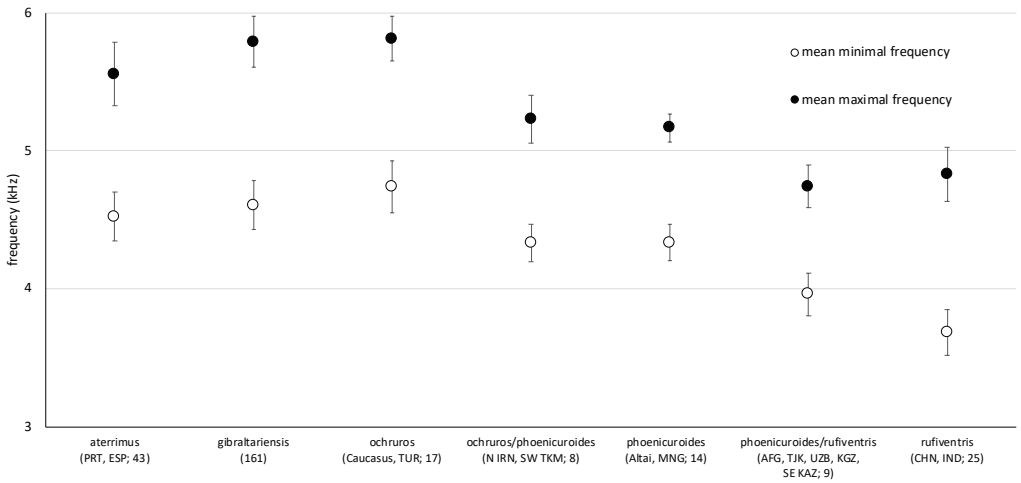

Figure 4. Mean min. and max. frequencies (± standard deviation) for the analysed subspecies and regions.

mirrors the initial section (forming a curve-like effect on a sonogram). These calls have a rather small range from the lowest to highest parts (Fig. 4) and are at lower frequencies than calls in the Altai and Mongolia: none exceeded 5.0 kHz (Table 1, Fig. 6). Unlike calls of the western subspecies and birds from the Altai and Mongolia, these calls sound rather like a very short constant *heed* to the human ear.

Finally, *rufiventris* has a call that is completely different from all other subspecies and locations, and is shared by all birds analysed from India (n = 10) and China (n = 15, overlap coefficient between these two regions = 0.75, Table 2). The main component of this call type is descending instead of rising and is at very low frequencies, with min. frequencies well

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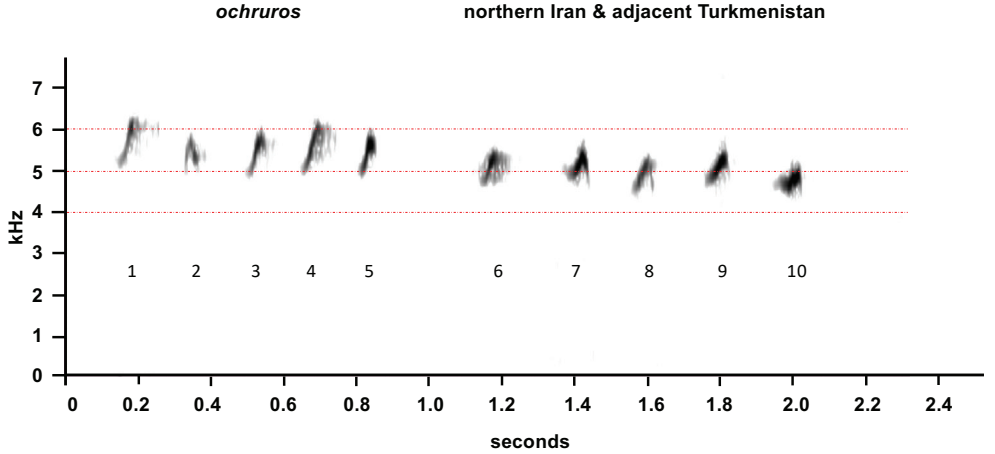

Figure 5. Variation in calls of *Phoenicurus o. ochruros* among birds from Turkey and the Caucasus (1–5) and those from northern Iran and adjacent Turkmenistan (6–10). 1: Turkey, 2020 (A. Calay), 2: Turkey, 2018 (Ö. Tutoğlu), 3: Georgia, 26 June 2005 (A. B. van den Berg; TSA), 4: Turkey, 30 May 2021 (Ü. Sevim; ML344076061), 5: Georgia, 21 June 2005 (A. B. van den Berg; TSA), 6: Iran, 27 June 2019 (S. Zirakjou; ML166096061), 7: Iran, 20 April 2017 (P. Åberg; XC404874), 8: Turkmenistan, 29 April 1996 (C. A. Boukreev; VPAV83626), 9: Turkmenistan, 3 April 1996 (C. A. Boukreev; VPAV83536), 10: Turkmenistan, 29 April 1996 (C. A. Boukreev; VPAV83629).

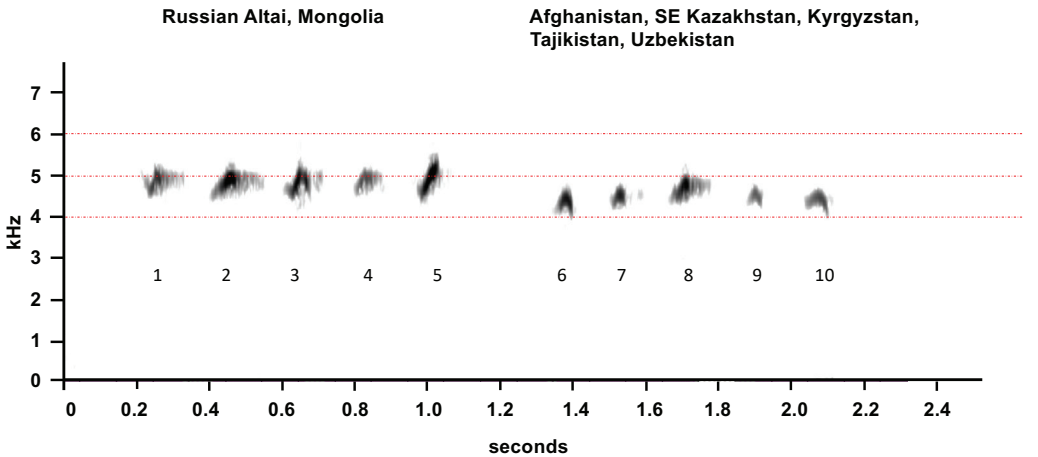

Figure 6. Calls of *Phoenicurus ochruros phoenicuroides* from the Altai and Mongolia (1–5) and from Afghanistan, Tajikistan, Kyrgyzstan, and south-east Kazakhstan (6–10). 1: Siberia, Russia, 24 June 2010 (A. Lindholm; XC158171), 2: Siberia, Russia, 4 May 1975 (B. N. Veprintsev, VPAV77651), 3: Siberia, Russia, 15 June 2011 (R. V. Konstantinowich, VPAV215085), 4: Mongolia, summer 2021 (J. Nergui), 5: Mongolia, 6 June 2013 (P. Franke; XC162680), 6: Tajikistan, 4 May 1968 (B. N. Veprintsev, VPAV75964), 7: Kyrgyzstan, August 2021 (F. Schneider), 8: Kazakhstan, 7 April 2011 (P. Franke; XC120341), 9: Tajikistan, 6 May 2018 (R. Martin), 10: Tajikistan, 16 May 2018 (R. Martin).

below 4.0 kHz (Table 1, Fig. 7). Max. frequencies were also low. Of the 25 birds, 20 gave calls below 5.0 kHz. *Rufiventris* calls were on average *c*.1.0 kHz lower than those of *aterrimus*, *gibraltariensis* and *ochruros*, a difference easily audible to the ear. Compared to calls from the southern range of *phoenicuroides*, the difference in frequency range is less obvious and the overlap coefficient is 0.37, but calls sound quite different because of the clearly audible descending part. The call is probably best described as a downward-inflected *tiut*. On a

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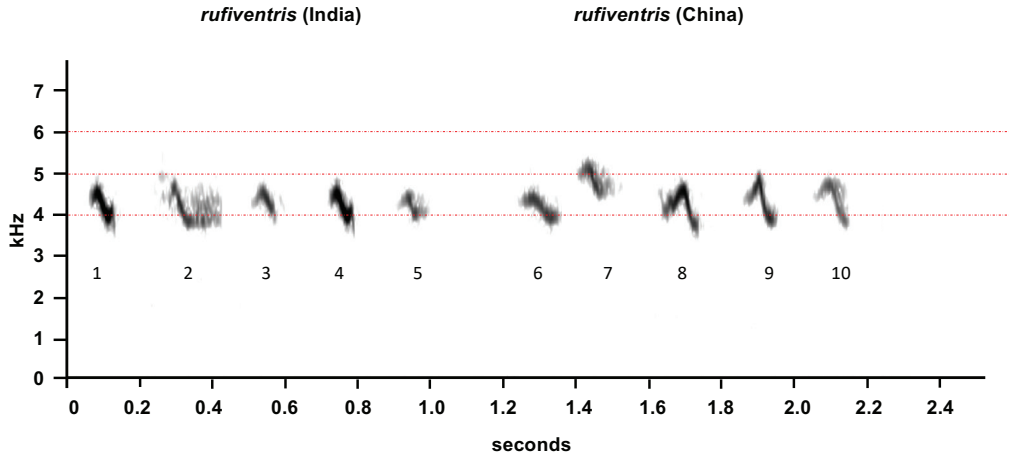

Figure 7. Variation in calls of *Phoenicurus ochruros rufiventris* from India (1–5) and Qinghai, China (6–10). 1: Jammu and Kashmir, 1 July 2019 (A. Spencer; XC547445), 2: Jammu and Kashmir, 1 August 2016 (P. Sharma; ML179434131), 3: Jammu and Kashmir, 9 July 2010 (P. C. Rasmussen; AV7604), 4: Jammu and Kashmir, 1 July 2019 (A. Spencer; XC547445; different bird to call 1), 5: Jammu and Kashmir, summer 2019 (C. Gasha), 6: Qinghai, 4 June 1997 (G. J. Carey; ML60498), 7: Qinghai, 27 June 2011 (M. Kennewell; ML201540771), 8: Qinghai, 11 July 2019 (P. Boesman; XC491392), 9: Qinghai, 8 July 2019 (P. Boesman; XC491388), 10: Qinghai, 29 June 2021 (Tao Liu; ML388969111).

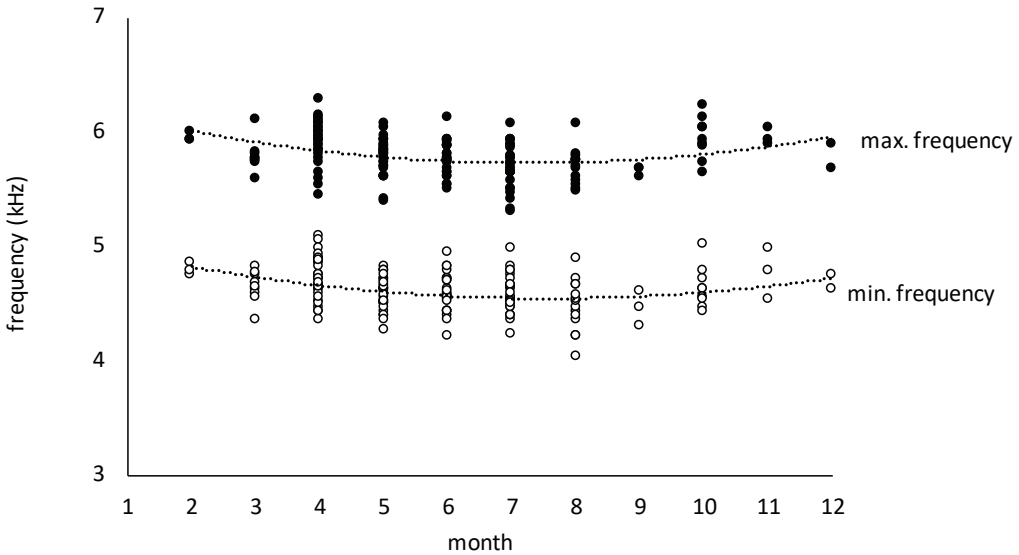

Figure 8. Seasonal variation in min. and max. frequency in *Phoenicurus ochruros gibraltariensis* calls (max. frequency: y = 10144x2 - 146.89x + 6260.6; R^2 = 0.1171; min. frequency: y = 8.9545x^2 – 135.11x + 5056.7; R^2 = 0.1139).

sonogram, there is a small rising 'hook' before the main descending part. In many birds, the call ends with a small inverted 'hook' on the sonogram (Fig. 7).

Seasonal variation.—Only for *gibraltariensis* was the sample large enough to analyse potential seasonal variation. Mean measurements were *c*.0.1–0.15 kHz lower in summer (*n* = 70) than in autumn (*n* = 15), winter (*n* = 5) and spring (*n* = 70) (Fig. 8).

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Discussion

Call groups and subspecies ranges.—Based on our results, there are three distinctive call types/groups (Fig. 9). The first group gives a rising *vist* call and is formed by *aterrimus*, *gibraltariensis*, *ochruros* (note that the latter is regarded as intermediate between Western and Eastern Black Redstarts in plumage) and northern *phoenicuroides* from the Altai and Mongolia (Eastern Black). The second group is formed by birds from the southern range of *phoenicuroides* that have *heed* calls, which are mostly given at lower frequencies and within a smaller frequency range than birds in group 1. A third group, whose calls appear specific to *rufiventris*, utters a distinctive descending low-frequency *tiut*. All three groups show very low (1 vs. 2: 0.03; 1 vs. 3: 0.00) or rather low overlap coefficients (2 vs. 3: 0.37), but note that sample size is rather small for some taxa. Glutz von Blotzheim (1988), Shirihai & Svensson (2018) and Collar (2021) assigned all Iranian birds to *ochruros*, except breeders at the border between Turkmenistan and Iran, which are assigned to *phoenicuroides*. Sangster (2021) treated all Iranian birds as *ochruros* whereas Fedorenko (2018) assigned them all to *phoenicuroides*. Our results are in line with the presence of a contact zone between *ochruros* and *phoenicuroides* in eastern Iran and adjacent Turkmenistan. We must highlight that we were unable to access a recording of the Levantine subspecies *semirufus*. Because this subspecies neighbours *ochruros* and approaches *phoenicuroides* in plumage but is smaller (Shirihai & Svensson 2018), it would be interesting to discover what their calls sound like. Furthermore, at least in *gibraltariensis* calls seem to be slightly lower pitched in summer. We have not examined the underlying reasons for this, but speculate it might be linked to breeding stress or age. Geographical variation within the third group seems to be small to non-existent, with birds from India (mainly Jammu and Kashmir) and China (Qinghai) showing no apparent differences and high overlap coefficient. Note that the Chinese sample includes birds from the ranges accorded to *P. o. xerophilus* (Stegmann 1928, Glutz von Blotzheim 1988) and *P. o. pleskei* (Fedorenko 2018), although both taxa are considered

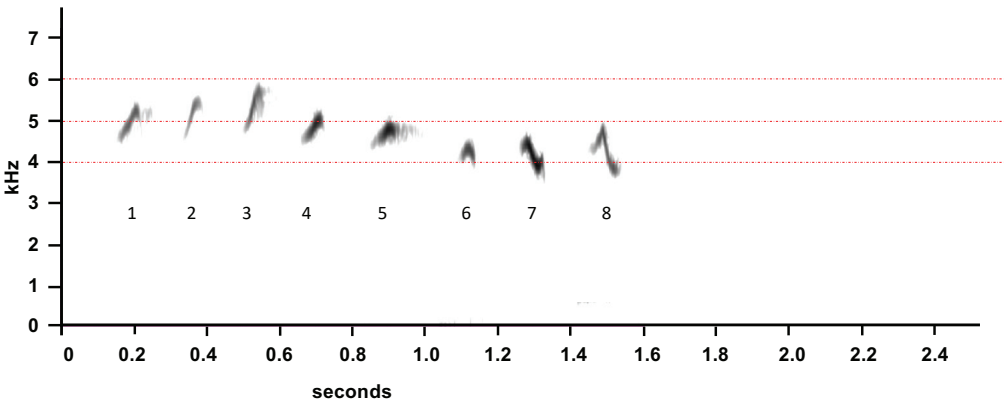

Figure 9. Examples of calls of *Phoenicurus ochruros aterrimus* (1), *P. o. gibraltariensis* (2), *P. o. ochruros* (3), a bird from northern Iran (4), a bird from the northern range of *P. o. phoenicuroides* (5), one from the south-eastern range of *P. o. phoenicuroides* (6), *rufiventris* from Jammu and Kashmir (7) and *rufiventris* from China (8). 1: Spain, 29 March 2012 (P. Åberg; XC148957), 2: England, 14 April 2021 (J. Spinks; XC638960), 3: Turkey, 30 May 2021 (Ü. Sevim; ML344076061), 4. Turkmenistan, 3 April 1996 (C. A. Boukreev, VPAV83536), 5: Siberia, Russia, 24 May 2021 (B. N. Veprintsev; VPAV77651), 6: Tajikistan, 4 May 1968 (B. N. Veprintsev; VPAV75694), 7: Jammu and Kashmir, 1 July 2019 (A, Spencer; XC547445), 8: Qinghai, China, 8 July 2019 (P. Boesman; XC491388).

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invalid by modern authorities. The second group contains birds from the contact zone between 'call type' groups 1 and 3: in Afghanistan, southern Kazakhstan, Kyrgyzstan, Tajikistan and Uzbekistan. Note that there is much confusion concerning subspecies limits here as well: Glutz von Blotzheim (1988), Ayé *et al*. (2012) and Sangster (2021) assigned all these to *phoenicuroides*, with *rufiventris* only from central India eastwards, whereas Fedorenko (2018) assumed that the limit between *phoenicuroides* and *rufiventris* lies much further west, in Tajikistan and Kyrgyzstan. Steijn (2005) and Shirihai & Svensson (2018) even considered birds as far west as Turkmenistan to be *rufiventris*. Steijn (2005), however, noted that populations with plumage intermediate between *phoenicuroides* and *rufiventris* occur in Tajikistan and the western Himalayas. Our own findings also suggest a broad contact zone in Central Asia. Small, grey-backed birds breeding in the Altai and Mongolia with low-pitched, rising *vist* calls (the newly described subspecies *murinus sensu* Fedorenko 2018; see below) and large, black-backed birds breeding in India and China (*rufiventris*) with low-pitched descending contact calls would thus form two ends of a continuum.

Combining our results based on calls with existing knowledge of subspecies limits based on plumages of adult males and size (Steijn 2005, Fedorenko 2018, Shirihai & Svensson 2018), separation into Western and Eastern Black Redstarts remains problematic, with *ochruros* not only occupying an intermediate position based on plumage but apparently sharing the call type of the western group. Furthermore, based on calls alone, *rufiventris* appears unique vs. all other forms (except potentially intermediate populations in Central Asia).

Recent mtDNA analyses recovered five distinct clades of Black Redstarts (Sangster 2021). However, these do not seem to match current subspecies limits, at least from Turkey eastwards. Comparing his results with our findings, no clear match between clades and call types is visible either. Note, however, that with a total of 66 birds analysed, the sample size in Sangster (2021) was rather small. Despite combining several published resources, there were no samples from southern Iberia, Iran, the Middle East, Central Asia and India. Analyses of more specimens and/or other genes including nuclear markers might yield further insights. Detailed analysis of song might also bear fruit, as there could be some differences between Western and Eastern birds in this respect (Martens & Eck 1995, Constantine *et al*. 2021). It bears mention that Common Redstart *P. phoenicurus* possesses several call types with a clear geographic pattern but this pattern does not always match subspecies limits, too (Martinez & Martin 2000, Martinez *et al*. 2022).

The validity of P. o. murinus.—Birds from the Altai and Mongolia are traditionally included in *phoenicuroides*, but Fedorenko (2018) proposed to treat these as a newly erected subspecies: *murinus*. His main rationale for this, based on a thorough analysis of photographs and specimens from various museums, was the invariably pure dark grey coloration of the head, nape and back, lacking any contrast in adult males, whereas the back is grey admixed black in adult males from more southerly locations in the range of *phoenicuroides*. However, the original description of *phoenicuroides* (Moore 1854) mentioned 'crown, neck, back and upper wing-coverts ash, with a rufous tint, the ash palest on the crown'. Its holotype, of which a photograph was published in Fedorenko (2018), also matches the description of *murinus*, a fact appreciated by the last-named author, whose main argument for describing northern populations as a new subspecies, was that the *phoenicuroides* holotype was collected on 21 March 1852 in its supposed winter quarters in Pakistan, thus its breeding location was unknown. Whilst our results reinforce the relative uniqueness of Black Redstarts in the Altai and Mongolia, we are hesitant to employ a new name for these birds, as we assume that the *phoenicuroides* holotype probably belongs to this population. In this case, *murinus* would be a junior synonym of *phoenicuroides* and it would be southern populations that would require a new name.

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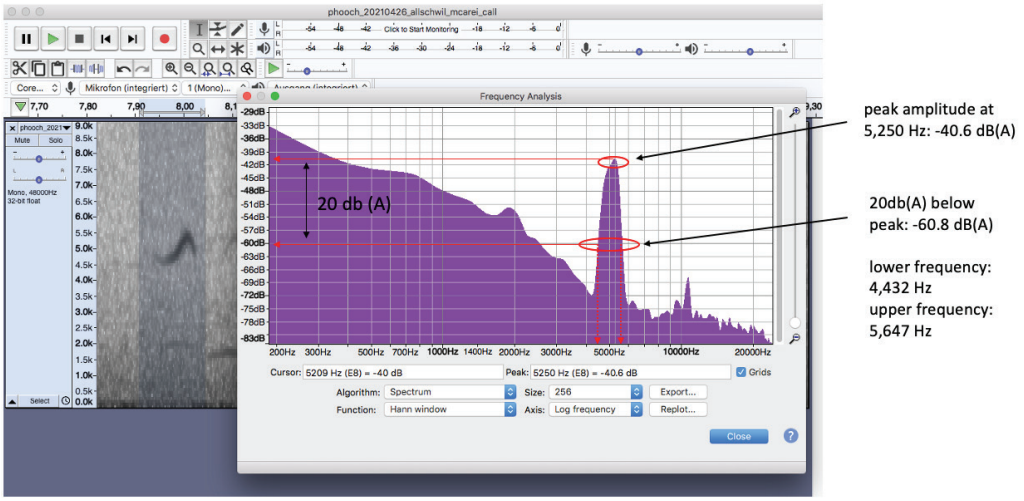
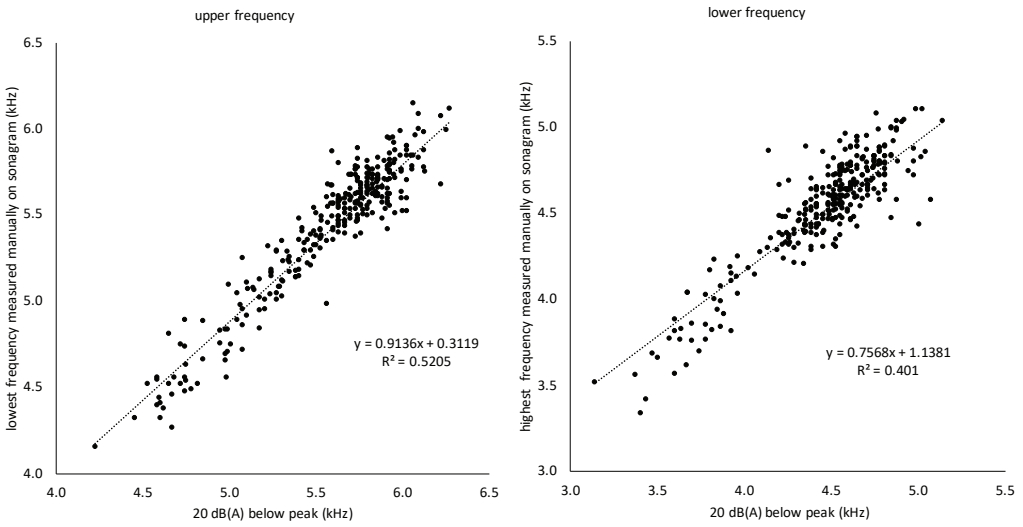
Appendix 1: method used to calculate lower and upper frequencies of calls with a standard decibel threshold of –20 dB (A) using Audacity ®. An example of a *Phoenicurus ochruros gibraltariensis* call from Switzerland is visualised here.



Appendix 2: comparison of methods used to define lower (left) and upper (right) frequencies for all records used herein.



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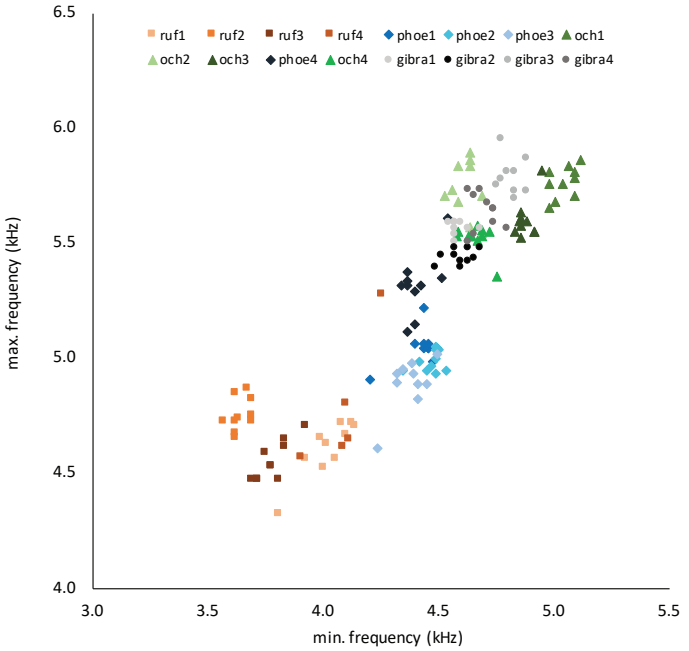
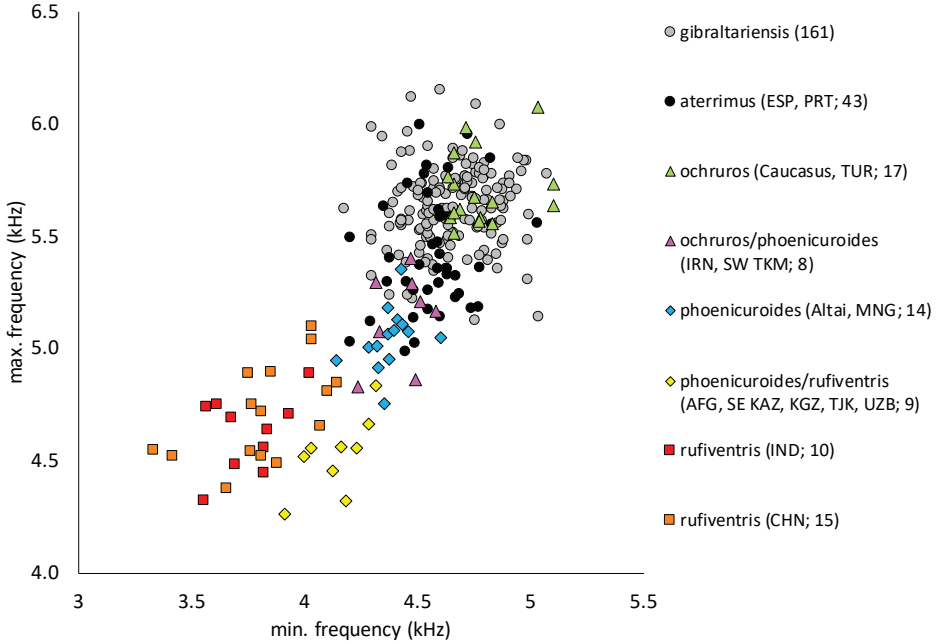
Appendix 3: individual variation in calls of *Phoenicurus ochruros rufiventris* (‘*ruf*’), *P. o. phoenicuroides* (‘*phoe*’), *P. o. ochruros* (‘*och*’) and *P. o. gibraltariensis* (‘*gibra*’). Four birds with ten manually measured calls are shown for each subspecies.



Appendix 4: plotted lower and upper frequencies based on manually measured values for all analysed birds, cf. Fig. 3. Countries are indicated by their official ISO-3166 three-letter codes.



Supplementary material: Recordings used for this paper including subspecies (according to the nomenclature used herein), country or region, database and recordist (including usernames from internet databases).

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