

# Geographical variation in Common Redstart calls

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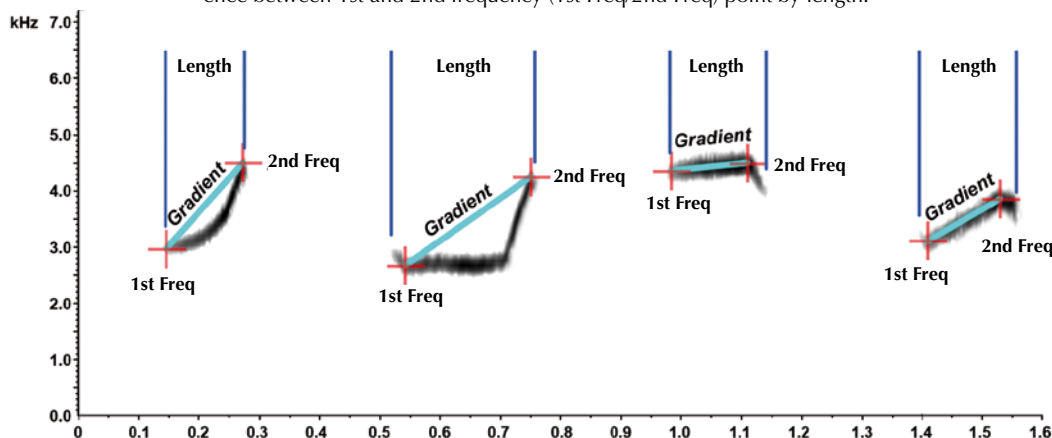
Common Redstart *Phoenicurus phoenicurus* occurs in two subspecies. Nominate *P p phoenicurus* (hereafter *phoenicurus*) breeds across most of the species' range, from Morocco, Spain and Britain in the west to lake Baikal, Russia, in the east. The other subspecies, Ehrenberg's Redstart *P p samamiscus* (hereafter *samamiscus*), has a south-easterly distribution. Its occurrence stretches from eastern Anatolia, Turkey, the southern Caucasus and the Middle East to south-western central Asia (Glutz von Blotzheim & Bauer 1988, Clement & Rose 2015). However, some authors include the whole of Turkey and central Asia in the breeding distribution range of *samamiscus* (Roselaar 1995, Kirwan et al 2008, Shirihai & Svensson 2018). Birds in the Balkan, Crimea and the northern Caucasus may show a mix of features and some consider these to be intergrades between the two subspecies (Glutz von Blotzheim & Bauer 1988, Svensson 1992, Kirwan et al 2008, Martinez 2010, Clement & Rose 2015); more research is needed. Adult males of both subspecies are identified by the presence (*samamiscus*) or absence (*phoenicurus*) of a white wing patch. Given good views, most first-winter males can be identified on other plumage characters, too (Small 2009). Identification of females based

on plumage features is only tentative (Small 2009, Clement & Rose 2015, Shirihai & Svensson 2018). Additionally, contact calls were thought to be a reliable identification feature for some time (Bergmann et al 2008, Small 2009, Ayé et al 2012, Svensson et al 2015): *phoenicurus* was meant to invariably utter a rising, slightly dissyllabic, *huid*, whereas the analogous call of *samamiscus* was described as a *heed* with constant frequency. It was generally assumed that *phoenicurus* shows the *huid* call across its whole range, until phenotypic *phoenicurus* with *heed* calls were observed in the east of its breeding range (Ayé et al 2014). In this study, we analysed calls of Common Redstarts from most parts of its breeding range to get more information about the distribution of the different calls.

## Methods

We collected sound recordings of Common Redstarts (in total 287 individuals). The main source for recordings was [www.xeno-canto.org](http://www.xeno-canto.org) (recordings of 127 individuals). We considered all recordings of calls available from the breeding period (May-July) published on this website by the end of July 2019. We added six birds of *samamiscus* from the second half of April, which sang the

FIGURE 1 Illustration of how measurements were taken from sonagrams for different call variants. Red crosses mark position from which we noted time and frequency. Gradient (blue line) was calculated by dividing frequency difference between 1st and 2nd frequency (1st Freq/2nd Freq) point by length.



## Geographical variation in Common Redstart calls



FIGURE 2 Variation of different types of calls of Common Redstart *Phoenicurus phoenicurus*. **1** Typical example of *huid* call in central Europe. Most of recorded *huid* calls strongly resemble this and following example. Male, Gütersloh, Germany, 9 June 1987 (*Klaus Conrads; TSA 0148*); **2** female, Lombardia, Italy, 27 May 2016 (*Francesco Sottile; XC318770*); **3** extraordinary steep example, Hautes-Alpes, France, 17 May 2011 (*Peter Boesman; XC270190*); **4** Staffordshire, England, 6 May 2018 (*Dominic Garcia-Hall; XC414853*); **5** female, Cheboksary, Russia, 22 June 2013 (*Albert Lastukhin; XC139395*); **6** especially birds from eastern distribution range showed very pronounced difference in gradient between beginning and end of call. Korgalzhyn, Kazakhstan, 3 May 2013 (*Thijs Fijen; XC145071*); **7** moreover, two of three birds from Mongolia had downward inflected end. Tereldsh, Mongolia, 11 June 1979 (*Dieter Wallschläger*); **8** this and three following calls are examples of commonest call variant in Italy north to Alps. Toscana, Italy, 15 June 2011 (*Marco Dragonetti; XC118530*); **9** Calabria, Italy, 3 July 2015 (*Francesco Sottile; XC254972*); **10** Italy, May 2011 (*Simona Inaudi; ornitho.it*); **11** Ticino, Switzerland, 30 June 2011 (*Tanya Harvey Ciampi; Youtube*); **12** Huelva, Andalucía, Spain, May (*Alberto Plata Ortiz*); **13** this and following recording show extraordinary records of *heed* calls in terms of geography. Stromberg, Rheinland-Pfalz, Germany, 15 June 2015 (*Frank Holzapfel; XC254143*); **14** Dividal, Troms, Norway, 23 June 2011 (*Stein Ø Nilsen; XC92981*).

typical song of this subspecies (based on Ayé et al 2014) and therefore likely defended a territory (southern birds arrive earlier at their breeding sites; Glutz von Blotzheim & Bauer 1988). In order to get a more representative collection from specific regions, additional material (number of individuals used given in parentheses) from May to July as well as from birds where videos proved that they were obviously breeding was included from: [www.youtube.com](http://www.youtube.com) (59 individual), own and privately shared recordings (38), [www.facebook.com](http://www.facebook.com) (17), [www.macaulaylibrary.org](http://www.macaulaylibrary.org) (13), several ornitho-platforms (12; Austria, France, Germany, Italy, Spain, Switzerland), [www.tierstimmenarchiv.de](http://www.tierstimmenarchiv.de) (7), [www.observation.org](http://www.observation.org) (3), [www.hbw.com/ibc](http://www.hbw.com/ibc) (1), [www.tarsiger.com](http://www.tarsiger.com) (2), [www.vimeo.com](http://www.vimeo.com) (2), [www.mdahlem.net](http://www.mdahlem.net) (1), [www.birdsong.it](http://www.birdsong.it) (1)

and [www.sounds.bl.uk](http://www.sounds.bl.uk) (1). We determined the call variant(s) for each recording by listening to the recording and checking the sonagram. Therefore, all recordings were converted to 44 kHz wav files (16 bit). Sonagrams were made with Raven (Bioacoustics Research Program 2014). We used Kaiser-Window to visualize the calls in combination with a sample overlap of 95% and a DFT size of 500 samples.

We categorised the calls qualitatively based on previous described categories (*huid* and *heed*), and if that was not possible, we made new categories. For a definition of the call variants see section 'Results'. Just one recording was considered if several recordings of the same call variant at the same site in the same year were available, unless it was clear that different birds were involved.

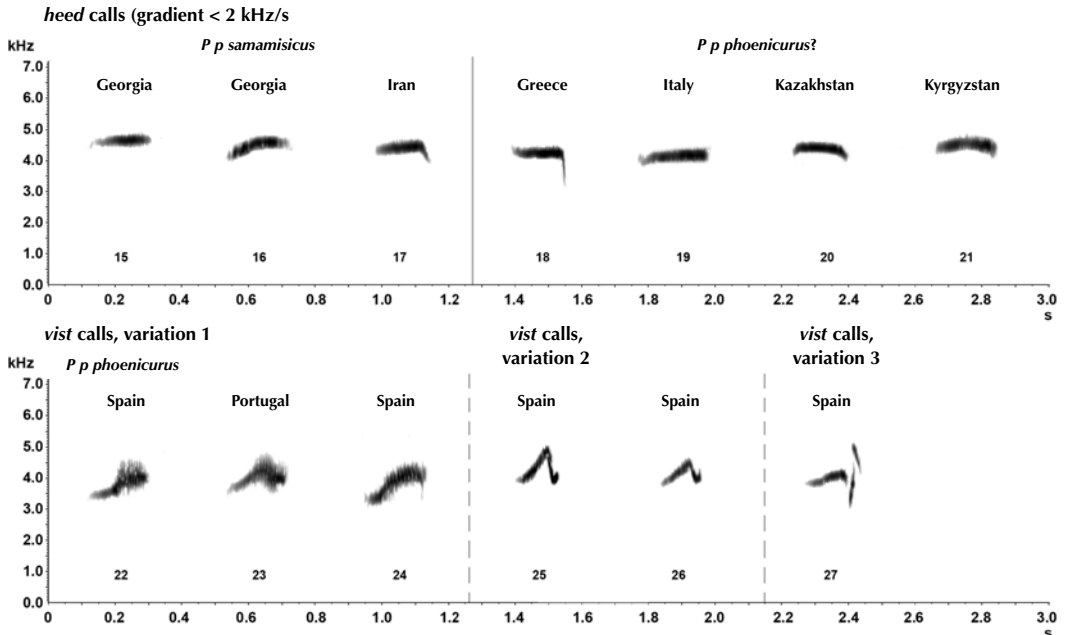


FIGURE 2 (continued) **15** male, Samtskhe-Javakheti, Georgia, 6 July 2013 (*Jarmo Pirhonen*; XC142822); **16** one out of only three rising *heed* calls from breeding range of *P p samamiscus*, still quite ‘flat’ in sonagram. Georgia, 31 May 2018 (*Aslan Bolkvadze*; Facebook); **17** Roodbarak, Mazandaran, Iran, 15 April 2017 (*Patrik Åberg*; XC405281); **18** this call was recorded in supposed intergradation zone. Male bird showing features of *P p samamiscus*, Thrace, Greece, 16 May 1976 (*Hans-Heiner Bergmann*); **19** following three calls show constant *heed* calls from *P p phoenicurus* breeding ranges. Bird from call 19 is same bird as in plate 220. Teramo, Abruzzo, Italy, 28 May 2016 (*Dimitri Marrone*; XC318906); **20** this bird switched regularly between these *heed* calls and typical *huid* calls. Astana, Kazakhstan, 4 July 2015 (*Youtube*); **21** Ala Archa NP, Kyrgyzstan, 18 May 2015 (*Ralph Martin*; XC312877); **22** male, Gijón, Asturias, Spain, 24 May 2011 (*Youtube*); **23** female, Lisboa, Portugal, 17 May 2009 (*Magnus Robb*); **24** Lugones, Asturias, Spain, breeding period 2014 (*Vimeo*); **25** note pronounced downward inflection at end of call, which is typical for *vist* variant type 2 and 3. Andalucía, Spain, 19 May 2015 (*José Carlos Sires*; XC274770); **26** Andalucía, Spain, 7 June 2015 (*José Carlos Sires*; XC279476); **27** Andalucía, Spain, 21 May 2016 (*José Carlos Sires*; XC319577).

In a statistical analysis, we tested for sexual and geographical differences in the calls. Therefore, we took several measurements (figure 1) and calculated the gradient (kHz/s) of the call by dividing the difference between 1st and 2nd frequency through the timespan. As calls within individuals were relatively stable, we chose one representative call per individual for testing. We fitted a linear model to the measurements of the *huid* calls (101 sexed and 96 unsexed individuals) and another one to the measurements of the *heed* calls (23 sexed and 44 unsexed individuals), using the ‘lm’ function of the statistics package of R (R Core Team 2016), to check for differences of the calls between sexes as well as geographic differences. We checked various diagnostics of model validity and stability. The fit of the models met the assump-

tions of normality and homogeneity of residuals (Quinn & Keough 2002, Field 2005). We analysed the influence of longitude, latitude, their interaction and sex on the gradient of the call, 1st and 2nd frequency and call length.

## Results

### Call variants of Common Redstart

We analysed 287 individuals, covering most parts of the species breeding range. The following call variants were detected: rising *huid*, rising or constant *heed* calls and three variants of a *vist* call (figure 2). *Huid* and *heed* calls are well known but the variability of *heed* calls was much higher than previously known. For a few calls it was thus far from straightforward to assign them to either vari-

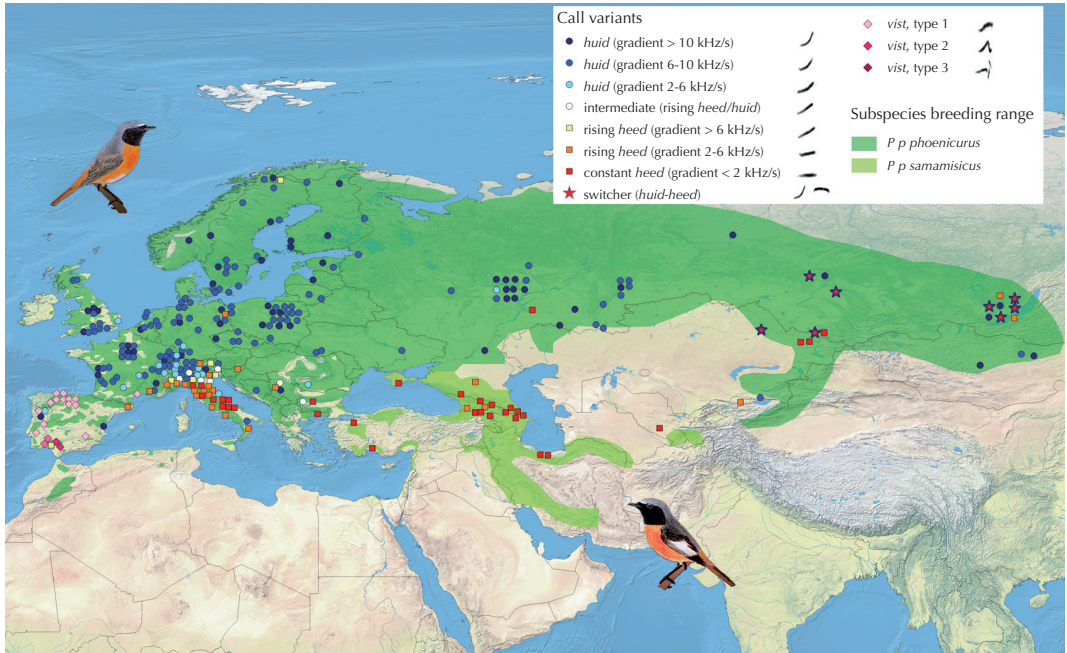


FIGURE 3 Distribution of call variants across breeding range of Common Redstart *Phoenicurus phoenicurus*. Each marker corresponds to an individual. If markers covered each other, we slightly shifted points to retain visibility. Map sources: www.birdlife.com (breeding range) and Natural Earth (www.naturalearthdata.com, background, countries). Subspecies ranges based on Shirihaï & Svensson (2018); note, however, that some authors consider birds of Balkan peninsula and western Turkey to be intergrades. Note that there are no recordings for one individual from Altai mountains and one from lake Baikal, that were switching between *huid* and *heed* call variants (Raffael Ayé & Balduin Fischer pers comm). As stated in text, recording quality of three birds from Spain labelled as *vist* type 1 does not allow to decide if their calls are better assigned to *vist* or *heed* calls.

ant (*huid* or *heed*) and some had to be classified as intermediate. We have retained the two variants, however, as the calls in previous publications were classified as such. *Vist* calls had not been described before to our knowledge. Call variant was stable within an individual, with the exception of at least eight birds from Kazakhstan and Russia switching between *huid* and *heed* calls. All call variants were regularly combined with ticking alarm calls and do not seem to differ in this respect.

#### Rising *huid* call

This is the classic call of *phoenicurus* that central and northern European birdwatchers are familiar with and can be best described by *huid*. All but three birds ( $n=170$ ) used *huid* calls (98%, figure 3) within the breeding area of *phoenicurus* in Central Europe north of the Alps, Britain, Fennoscandia and European Russia. The call is clearly uprising (similar to the contact call of Willow Warbler *Phylloscopus trochilus*), with a mostly low starting

frequency. Gradient increases towards the end of the call, which makes the call sound disyllabic. In the linear model, sex had no significant effect on the measured values. Therefore, we ran another model without 'sex' as a covariate to increase the sample size by using the unsexed birds as well. Latitude and longitude showed significant effects on gradient, 1st and 2nd frequency and call length (appendix 1 and 2). Gradient increased from south-west to the north-east while call length increased from south-east to north-west (appendix 3). 1st frequency was highest in the south-east and lowest in the north-east, while 2nd frequency was lowest in the south-west and north-east and highest in the north-west and south-east.

#### Heed call

The *heed* calls form a line with a constant, rising or slightly decreasing gradient when visualised in a sonagram. Calls given at constant frequency (reminiscent of the slightly higher pitched contact calls of Collared Flycatcher *Ficedula albicollis*) are



FIGURE 4 'Switcher', using *huid* and *heed* calls. Adult, female, same bird as in plate 221. Mikhaylovka, Irkutsk Oblast, Russia, 19 June 2019 (Ralph Martin).

known as the typical *samamiscus* call. We found only this call type from the breeding range of *samamiscus* ( $n=20$ ; two calls showed a gradient  $>2.0$  kHz/s, none exceeded 4.0 kHz/s), but also on the Balkan and in Italy including adjacent regions from Austria, southern France and Switzerland. *Heed* calls with a rising gradient are especially widespread in the southern Alps with a fluent transition to *huid* calls with a small gradient. As a consequence, several calls had to be classified as intermediate (Alps, northern Balkan, figure 3). Rise in pitch of *heed* calls become roughly audible when starting and ending frequency differ by at least 0.3 kHz (but note that there are substantial differences between observers in this respect). *Heed* calls were also detected in Kyrgyzstan close to the south-eastern border of the *phoenicurus* range, and in the Russian Far East and Kazakhstan, where several birds combined this call type with the *huid* call ('switchers' in figure 3-4).

In the linear model, sex had no significant effect on the measured values, but sample size was very small ( $n=23$ ). However, as sex had no significant effect for the *huid* calls either, we ran another model without 'sex' as a covariate to increase the sample size by using the unsexed birds as well. Latitude and longitude showed significant effects on gradient, 1st and 2nd frequency but not on call length (appendix 4 and 5). Gradient increased while 1st and 2nd frequency decreased from south-east to north-west (appendix 6).

#### Variations of *vist* calls

We found highly differing calls in Iberia (plus one call from adjacent south-western France). Here, Common Redstart is patchily distributed and restricted to mountainous regions, especially in the south (see figure 3). Some birds showed intermediate calls between *heed* and *huid* but with a

rough or hoarse sounding in some, thanks to a quickly modulated uprising call (*vist* variation 1). Most south-western calls (*vist* variations 2 and 3) had a prominent downward inflection in the end in common (calls reminded a Common Chiffchaff *Phylloscopus collybita* with *sweo* calls), and some showed even further uprising and decreasing elements (variation 3). These calls are reminiscent of calls of Black Redstart *P. ochruros* but are given at lower frequencies (*vist* calls in Common Redstarts start at frequencies between 3.0 and 3.8 kHz, the highest point in the sonagram equalled 4.4-5.2 kHz. Contrarily, Black Redstart calls range roughly from 4.5 up to 6.0 kHz at the highest point). A total of three recordings from Spain (2) and Portugal (1) with low recording quality sound similar to *heed* calls (and maybe they are) but recording quality is not sufficient to exclude further variants of *vist* calls.

#### Discussion

In this study, we analysed call variation of Common Redstart of most parts of its distribution range. *Phoenicurus* of the north-western population uttered almost exclusively *huid* calls. Birds from the *samamiscus* breeding range only used *heed* calls and the majority of calls of *samamiscus* showed almost no gradient. We found birds giving *heed* calls on the Balkan (in line with the hypothesis of an intergradation zone in this region; Matvejev & Vasi 1973, Clement & Rose 2015) and even in southern France and, more so, on the Italian peninsula, where surprisingly few birds with *huid* calls were recorded (just two *huid* callers out of 17 birds from Italy south of Genova). Calls of some of these *heed* calling birds were identical to calls that were considered to be typical of *samamiscus*. In these regions, at least from time to time, unusual birds with rather prominent white wing patches seem to occur, and some were



**220** Common Redstart / Gekraagde Roodstaart *Phoenicurus phoenicurus phoenicurus*, second calendar-year male, Teramo, Abruzzo, Italy, 24 April 2016 (Dimitri Marrone). This breeding bird repeatedly gave constant *heed* calls (cf figure 2, call 19). Note that it has lost its tail. Most *P p samamisticus* of same age show some whitish base to secondaries (Small 2009). **221** Common Redstart / Gekraagde Roodstaart *Phoenicurus phoenicurus phoenicurus*, adult female, Mikhaylovka, Irkutsk Oblast, Russia, 20 June 2019 (Ralph Martin). Only female in our study that switched between *huid* and *heed* calls was this male-like coloured bird (cf figure 4). **222** Common Redstart / Gekraagde Roodstaart *Phoenicurus phoenicurus phoenicurus*, adult male, Sierre de las Nieves, Andalucía, Spain, 30 May 2016 (Ricky Owen). Bird from southern Iberia, whose breeding birds give highly distinct *vist* call variants 2 and 3.

claimed to be *samamisticus*. According to Small (2009), seven claims come from southern France, but none was sufficiently documented to exclude any *phoenicurus* with extensive pale fringing on secondaries and, subsequently, the French rarities committee has not accepted them (Frédéric Jiguet pers comm). There are two records of *samamisticus* in Italy. The first, a bird from Lampedusa on 26 September 2007, mentioned in Ruggieri & Sighele (2008), Small (2009) and Clement & Rose (2015), should possibly be re-evaluated in light of new knowledge (Andrea Corso pers comm; see also rejected bird in the Netherlands, cf Wassink & Ebels (2005)). The second has been caught at a

ringing station on the small Pontine island Ventotene on 2 May 2019 ([www.ornitho.it/index.php?m\\_id=54&backlink=skip&mid=289548](http://www.ornitho.it/index.php?m_id=54&backlink=skip&mid=289548), Jacopo Barchiesi pers comm). With only one or two certain records from the region, it is reasonable to assume that pure *samamisticus* are at least genuinely rare in southern France and Italy and the high proportion of *heed* callers here is unlikely to be explained by *samamisticus* vagrants. Furthermore, it is worth emphasizing that some of the Italian birds giving *heed* calls (constant and rising) were photographed or filmed, and none of the males showed a prominent white wing panel as would be expected in adult *samamisticus*. We

thus exclude the possibility that these birds were pure *samamiscus*. However, the increase of the gradient of the *heed* calls to the north-west might be a hint for introgression of *samamiscus* into *phoenicurus* in the Balkan and Italy (if calls are inherited in the Common Redstart). Hogner et al (2012) analysed mtDNA in Common Redstart. Unfortunately, their markers did not separate *phoenicurus* and *samamiscus* but Ertan (2002) used methods which showed differences between both subspecies but also high gene flow between them, supporting a large mixing zone. It is possible that the corresponding locus or loci for call inheritance can introgress independently from plumage patterns. Typically, morphological characters are used to distinguish between subspecies but here they do not seem to be conclusive, as the line between *phoenicurus* and *samamiscus* is drawn very differently by different authors (including the Balkan as large contact zone in Clement & Rose (2015) while Shirihihi & Svensson (2018) define birds in western Turkey as intergrades) or to be obscured by second calendar-year male *samamiscus* with juvenile primaries that may have been sometimes misidentified as *phoenicurus*.

In eastern regions, where *samamiscus* and *phoenicurus* might get in contact on migration or thanks to overshooting birds, *heed* calls occur as well (in the Altai, Ayé et al 2014; Tian-Shan, lake Baikal and north of the Caspian Sea, figure 3). Surprisingly, birds able to switch between *huid* and *heed* calls occur there. While in the beginning, it seemed that the description of two such birds was more unusual (Ayé et al 2014), we were now able to find a total of eight such ‘call switching’ birds (almost half of the birds recorded in the Far East). Indeed such birds might be often overlooked, as at least some birds seemed to switch between the two calls only when they were very agitated. With little agitation, however, just one call variation was uttered and they would have been classified as typical *huid* or *heed* callers during a brief encounter. This leads us to conclude that call switching from *huid* to *heed* occurs regularly in Far Eastern populations. While we did not find any hint of such call switching in Western Europe during our analyses, NM found one female in Switzerland shortly before publication of the present article, that uttered few *heed* calls, but *huid* calls were the norm (XC562589). Thus, call switching may very rarely be present even in Western Europe.

Another unexpected finding for such a common species in Europe was the existence of calls in Iberia which are very different from the hitherto

described calls of Common Redstart. There might be a geographical pattern of the different *vist* calls, however, *vist* variation 2 and *vist* variation 3 calls were found close to each other with very small sample sizes and might be just a variant of the same call. We also do not know what the transition between these *vist* calls looks like, nor if the three *huid* calls and the two *heed* calls from Iberia (figure 3) were just from very late migrants or if these calls occur regularly here, too. Although *vist* calls of these Iberian birds are quite different from calls of all other *phoenicurus* populations, we noticed that song does not differ in length and variability of the introductory part. Thus, we agree with the findings of Ayé et al (2014) that song in *phoenicurus* seems to be very constant across the whole breeding range.

To sum up, it would be interesting to obtain more recordings of Common Redstart calls of breeding birds from the Iberian Peninsula and, even more, from the Maghreb as well as from the south-eastern *phoenicurus* range in Kyrgyzstan and eastern Kazakhstan and westernmost China and from *samamiscus* birds from Tajikistan and Uzbekistan.

## Conclusions

Following our data, *huid* calls seem to be restricted to *phoenicurus* as we found no *samamiscus* giving this call variant. Moreover, *heed* and especially rising *heed* calls seem to be common near contact zones of both subspecies. Variation of the calls of *phoenicurus* is larger than previously thought. We found undescribed call variants in Iberia and *heed* calls to be common in southern Europe, especially in Italy, perhaps originating from genetic introgression with *samamiscus* (maybe independent of plumage features). Thus, a *heed* calling Common Redstart can no longer be considered as a valuable *samamiscus* candidate or even an ‘Eastern Common Redstart’ anymore. We recommend that in central and western Europe, only very typical adult male birds should be recognized as *samamiscus* (features given in Small 2009). However, the documentation of less typical birds would be helpful to better understand the total variation and a thorough study of plumage characters in suspected intergradation zones of *phoenicurus* and *samamiscus* would be much appreciated.

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## Samenvatting

**GEOGRAFISCHE VARIATIE IN ROEP VAN GEKRAAGDE ROODSTAART** Gekraagde Roodstaart *Phoenicurus phoenicurus* heeft twee ondersoorten waarvan de nominaat *P p phoenicurus* (hierna *phoenicurus*) als broedvogel voorkomt in het grootste deel van het verspreidingsgebied, namelijk van Marokko, Spanje en Brittannië in het westen, tot het Baikalmeer, Rusland, in het oosten. De ondersoort *P p samamiscus* (hierna *samamiscus*) heeft een meer zuidoostelijke verspreiding. Adulte mannetjes van *samamiscus* zijn van *phoenicurus* te onderscheiden door de aanwezigheid van een witte vleugelvlek. Ook eerste-winter mannetjes zijn doorgaans goed te onderscheiden, maar een betrouwbare determinatie van vrouwtjes is niet mogelijk. Van het verschil in contactroep tussen beide ondersoorten werd aangenomen dat het een betrouwbaar kenmerk was. De contactroep van *phoenicurus* kan omschreven worden als een stijgend *hoe-wied*, terwijl de contactroep van *samamiscus* klinkt als een op gelijke toonhoogte blijvend *hied*. In dit artikel worden opnames van de contactroep uit vrijwel het gehele verspreidingsgebied van Gekraagde Roodstaart geanalyseerd om meer inzicht te krijgen in de variatie en verspreiding van de contactroep. In totaal werden hiervoor opnames gebruikt van 287 roepende individuen uit de broedperiode (mei-juli).

Naast de voor *phoenicurus* karakteristieke stijgende *hoe-wied*-roep, werden ook meerdere varianten van de *hied*-roep vastgesteld en een nog niet eerder beschreven *viest*-roep. In het noordwestelijke deel van het verspreidingsgebied van *phoenicurus* werd bijna alleen de kenmerkende *hoe-wied*-roep geregistreerd en in het verspreidingsgebied van *samamiscus* alleen de *hied*-roep. Binnen het verspreidingsgebied van *phoenicurus* werden op de Balkan zowel de klassieke *hoe-wied*-roep als meerdere varianten van de *hied*-roep vastgesteld en ook in Italië werd de *hied*-roep veel genoteerd en was veel variatie in die roep aanwezig. De niet eerder geregistreerde *viest*-roep werd vastgesteld op het Iberisch Schiereiland. Daarmee is de variatie in contactroep van Gekraagde Roodstaart groter dan gedacht, met name in het verspreidingsgebied van *phoenicurus*. De veelvuldig vastgestelde *hied*-roep in Italië kan afkomstig zijn van genetische introgressie met populaties van *samamiscus*. Daarmee is dus een *hied* roepende Gekraagde Roodstaart niet per definitie een kandidaat *samamiscus* als dit niet in de eerste plaats wordt ondersteund door verenkleedkenmerken.

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APPENDIX 1 Results of linear models of *huid* calls, including sex as covariate, as described under Methods. Significant p-values indicated with asterisk ( $p < 0.05 = *$ ,  $p < 0.01 = **$  and  $p < 0.001 = ***$ ).

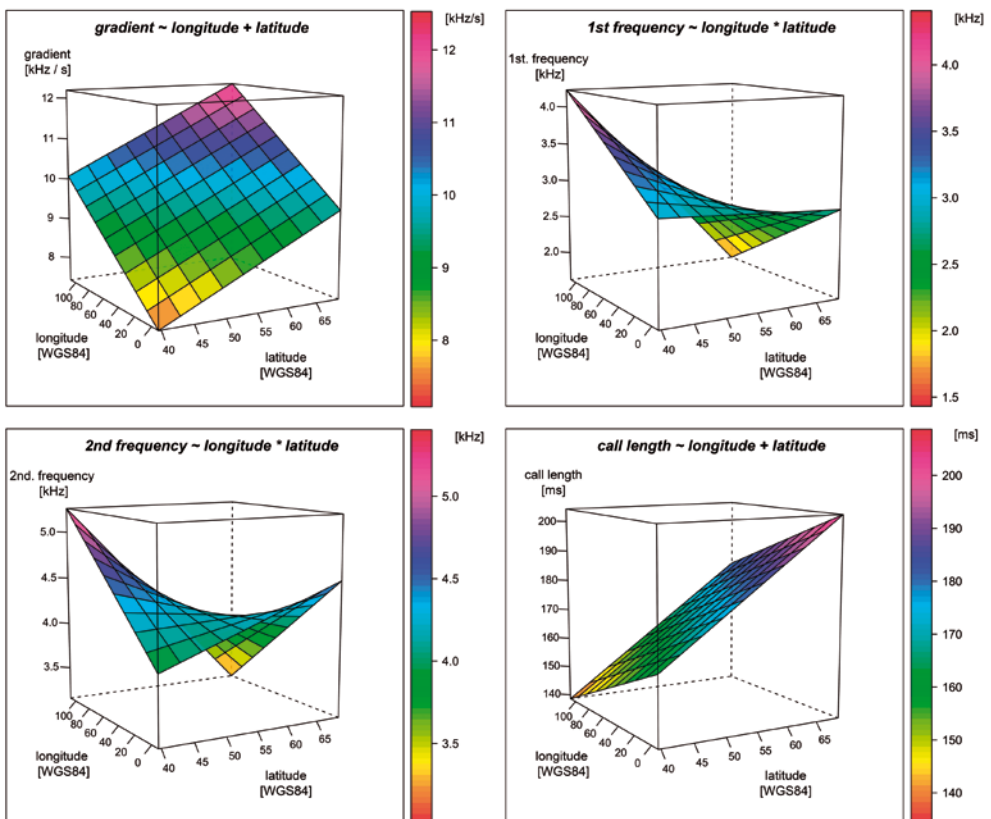
Response		estimate	standard error	t-value	p-value
<b>gradient</b>	intercept	-2.016	3.675	-0.549	0.585
	longitude	0.427	0.182	2.353	0.021*
	latitude	0.204	0.071	2.863	0.005**
	sexm	-0.405	0.416	-0.975	0.332
	interaction latitude:longitude	-0.008	0.003	-2.203	0.030*
<b>1st frequency</b>	intercept	3.190	0.321	9.919	0.000
	longitude	0.040	0.016	2.515	0.014
	latitude	-0.006	0.006	-0.962	0.338
	sexm	0.018	0.036	0.497	0.620
	interaction latitude:longitude	-0.001	0.001	-2.475	0.015*
<b>2nd frequency</b>	intercept	2.676	0.370	7.228	0.001***
	longitude	0.075	0.018	4.129	0.001***
	latitude	0.029	0.007	4.007	0.001***
	sexm	0.028	0.042	0.665	0.508
	interaction latitude:longitude	-0.001	0.001	-4.148	0.001***
<b>call length</b> (interaction longitude:latitude not significant and therefore excluded)	intercept	108.635	25.716	4.224	0.001***
	longitude	-0.211	0.141	-1.498	0.138
	longitude:latitude	1.300	0.493	2.634	0.010**
	sexm	5.678	5.998	0.947	0.346

## Geographical variation in Common Redstart calls

APPENDIX 2 Results of linear models of *huid* calls, excluding sex as covariate, as described under Methods. Significant p-values indicated with asterisk ( $p < 0.05 = *$ ,  $p < 0.01 = **$  and  $p < 0.001 = ***$ ).

Response		estimate	standard error	t-value	p-value
<b>gradient</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	4.716	1.381	3.416	0.001***
	longitude	0.023	0.006	3.856	0.001***
	latitude	0.073	0.027	2.698	0.001**
<b>1st frequency</b>	intercept	3.442	0.166	20.754	0.001***
	interaction latitude:longitude	-0.001	0.000	-6.051	0.001***
<b>2nd frequency</b>	intercept	3.254	0.223	14.571	0.001***
	interaction latitude:longitude	-0.001	0.000	-5.142	0.001***
<b>call length</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	101.202	17.926	5.646	0.001***
	longitude	-0.194	0.079	-2.473	0.014*
	latitude	1.473	0.348	4.231	0.001***

APPENDIX 3 Gradient, 1st frequency, 2nd frequency and call length of *huid* calls in dependency of longitude and latitude. Covariate 'sex' not included in figure as it was not significant.



APPENDIX 4 Results of linear models of *heed* calls, including sex as covariate, as described under Methods. Significant p-values indicated with asterisk ( $p < 0.05 = *$ ,  $p < 0.01 = **$  and  $p < 0.001 = ***$ ).

Response		estimate	standard error	t-value	p-value
<b>gradient</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	6.164	6.467	0.953	0.353
	longitude	-0.009	0.022	-0.408	0.688
	<i>longitude:latitude</i>	-0.059	0.156	-0.381	0.708
	sexm	-1.521	0.950	-1.601	0.126
<b>1st frequency</b>	intercept	1.092	1.337	0.817	0.424
	sexm	0.269	0.131	2.055	0.055
	interaction <i>longitude:latitude</i>	-0.001	0.001	-2.447	0.025*
<b>2nd frequency</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	4.430	0.549	8.059	0.001***
	longitude	0.001	0.002	0.175	0.863
	<i>longitude:latitude</i>	-0.004	0.013	-0.298	0.769
	sexm	0.004	0.081	0.049	0.961
<b>call length</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	117.834	87.780	1.342	0.197
	longitude	-0.464	0.302	-1.534	0.144
	<i>longitude:latitude</i>	1.892	2.136	0.886	0.388
	sexm	-12.895	12.605	-1.023	0.321

APPENDIX 5 Results of linear models of *heed* calls, excluding sex as covariate, as described under Methods. Significant p-values indicated with asterisk ( $p < 0.05 = *$ ,  $p < 0.01 = **$  and  $p < 0.001 = ***$ ).

Response		estimate	standard error	t-value	p-value
<b>gradient</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	-1.718	2.196	-0.782	0.437
	longitude	-0.044	0.009	-4.744	0.001***
	<i>longitude:latitude</i>	0.124	0.051	2.447	0.017*
<b>1st frequency</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	5.429	0.383	14.160	0.001***
	longitude	0.010	0.002	6.252	0.001***
	<i>longitude:latitude</i>	-0.041	0.009	-4.627	0.001***
<b>2nd frequency</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	5.348	0.252	21.212	0.001***
	longitude	0.004	0.001	3.589	0.001***
	<i>longitude:latitude</i>	-0.027	0.006	-4.682	0.001***
<b>call length</b> (interaction <i>longitude:latitude</i> not significant and therefore excluded)	intercept	206.322	26.121	7.899	0.001***
	longitude	0.028	0.109	0.254	0.801
	<i>longitude:latitude</i>	-0.930	0.605	-1.536	0.130

## Geographical variation in Common Redstart calls

APPENDIX 6 Gradient, 1st frequency, 2nd frequency and call length of *heed* calls in dependency of longitude and latitude. Covariate 'sex' not included in figure as it was not significant.

