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ORIGINAL ARTICLE

Resolving disputed subspecies distribution limits, and revealing intraspecific intergradation, in the Common Redstart *Phoenicurus phoenicurus* using citizen science and museum data

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Abstract
Contact zones with hybridization are documented for several Palearctic bird taxa. However, their extent is still poorly understood in many cases, including the Common Redstart *Phoenicurus phoenicurus*. Nominate *P. p. phoenicurus* breeds across most of the species' range, whereas *P. p. samamisicus* is restricted to the south-eastern part. Their precise distributions are disputed as is the existence and prevalence of hybridization between them within potential contact zones in the Balkans, Turkey and the Caucasus region. Adult males differ by the presence (*samamisicus*) or absence (*phoenicurus*) of a white wing patch; however, there is variation and white is lacking in most second-calendar-year males of both subspecies. Further, male *samamisicus* is thought to be darker on the mantle. We map the occurrence of pre-defined states in these two characters during the breeding season across the species' range based upon photos in online citizen science databases, subsequently complemented by an examination of museum specimens to refute or verify the pattern inferred from photos. We demonstrate that the extent of white in the wing varies throughout the range, but nevertheless is geographically structured. Adult breeders with a large white wing patch and black mantle occurred only in Greece, southern Bulgaria, Turkey, Crimea, and the Caucasus to Iran, which should be considered the breeding range of *samamisicus*. Earlier reports of intermediates and/or *phoenicurus* breeding there perhaps reflect confusion with second-year male *samamisicus.* Broad areas in the Balkans and north of the Black Sea were revealed as zones of intraspecific intergradation. Employing citizen science data enabled us to acquire a much larger sample than by using museum material alone. Although photographs from citizen science databases are unlikely to ever completely replace museum specimens, our approach of combining both types of data could prove a model for similar future research.

Keywords Citizen science · Common Redstart · Hybridization · Intergradation · *Phoenicurus* · Subspecies distribution

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Zusammenfassung

Umstrittene Verbreitungsgrenzen der Unterarten des Gartenrotschwanzes *Phoenicurus phoenicurus* und Ausmaß intraspezifischer Intergradation: eine Klärung mit Hilfe von Citizen Science-Daten und Museumssammlungen Kontaktzonen mit Hybridisierung sind für mehrere paläarktische Vogeltaxa dokumentiert. Ihre Ausdehnung ist jedoch in vielen Fällen noch unzureichend bekannt, so auch beim Gartenrotschwanz *Phoenicurus phoenicurus*. Die Nominatform *P. p. phoenicurus* brütet im größten Teil des Verbreitungsgebiets der Art, während die Unterart *P. p. samamisicus* auf den südöstlichen Teil beschränkt ist. Ihre genaue Verbreitung ist umstritten, ebenso wie die Existenz und das Ausmaß von Hybridisierung zwischen den beiden in potenziellen Kontaktzonen auf dem Balkan, der Türkei und der Kaukasusregion. Adulte Männchen unterscheiden sich durch das Vorhandensein (*samamisicus*) oder das Fehlen (*phoenicurus*) eines weißen Flügelspiegels; allerdings unterliegt dieses Merkmal deutlicher Variation und die meisten Männchen beider Unterarten im zweiten Kalenderjahr weisen gar kein Weiß im Flügel auf. Desweitern wird angenommen, dass die Männchen von *samamisicus* einen dunkler gefärbten Mantel aufweisen. Wir erfassten das Auftreten vordefinierter Kategorien dieser beiden Merkmale bei Männchen aus der Brutzeit im gesamten Verbreitungsgebiet der Art auf der Grundlage von Fotos in Citizen Science Online-Datenbanken. Diese wurden durch Daten von Museumsexemplaren ergänzt, um die anhand von Fotos erhaltenen Ergebnisse zu verifizieren. Unsere Resultate zeigen, dass das Ausmaß von Weiß im Flügel im gesamten Verbreitungsgebiet variiert, aber dennoch geografisch strukturiert ist. Adulte männliche Brutvögel mit einem großen weißen Flügelfleck und schwärzlichem Mantel kommen nur in Griechenland, Südbulgarien, der Türkei, der Krim und dem Kaukasus bis zum Iran vor. Diese Region sollte als das eigentliche Brutgebiet von *samamisicus* betrachtet werden. Frühere Berichte über brütende Männchen von *phoenicurus* oder intermediären Individuen in dieser Region betreffen wohl Verwechslungen mit Männchen von *samamisicus* im zweiten Kalenderjahr. Große Gebiete auf dem Balkan und nördlich des Schwarzen Meeres dagegen erwiesen sich als Intergradationszonen beider Unterarten. Die Nutzung von Citizen Science-Daten ermöglichte es uns, eine viel größere Stichprobe zu erhalten, als es durch die Berücksichtigung von Museumsmaterial allein möglich gewesen wäre. Fotos aus Citizen Science Datenbanken werden Museumsammlungen nie vollständig ersetzen können. Unser Ansatz, beide Arten von Daten zu kombinieren, kann aber als Modell für ähnliche zukünftige Forschung dienen.

Introduction

Many Palearctic bird taxa possess parapatric distributions accompanied by varying degrees of hybridization and introgression (Newton 2003; Price 2007). Often, this is considered a consequence of repeated range contraction and fragmentation, followed by periods of expansion during which secondary contact develops, resulting from cyclical climate fluctuations and associated environmental changes in the late Pleistocene (e.g., Hewitt 2000). One hotspot of secondary contact zones for Palearctic passerines has been revealed in the Middle East (Aliabadian et al. 2005). Such a contact zone between the two subspecies of the Common Redstart *Phoenicurus phoenicurus* might also be located in the north of this region.

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), northern Mongolia, and north-west China, in the east (del Hoyo and Collar 2016). The other subspecies, 'Ehrenberg's Redstart' *P. p. samamisicus* (hereafter *samamisicus*), is restricted to the south-eastern part of the species' distribution, with its core breeding range stretching across eastern Turkey, the southern Caucasus, and the Middle East to south-western Central Asia (Clement 2015; Glutz von Blotzheim 1988), perhaps as far east as north-west Afghanistan (Rasmussen and Anderton 2012) and (subspecies unclear) even western Pakistan (Roberts 1992; two specimens at the Natural History Museum, Tring, and one at the Bombay Natural History Society Museum, Mumbai). For more details on these specimens, see Kirwan et al. (2022). However, there is considerable debate concerning the precise extent of its breeding range. Although Small (2009) concluded that there was a "distinct lack of evidence of hybridisation" between the two subspecies, other authors have suggested that broad zones of intergradation occur. Especially, birds from the Balkans, Turkey, and the northern Caucasus have been reported to show mixed features, and consequently have been considered to be intergrades between the two subspecies (Glutz von Blotzheim 1988; Matvejev and Vasić 1973; Svensson 1992). Kirwan et al. (2008) broadly agreed with Svensson (1992) that Turkey might represent a zone of intergradation, but also specified that they had seen no museum material from the country both attributable to the nominate subspecies and definitely involving breeding birds. However, still other commentators have considered all of Turkey (del Hoyo and Collar 2016; Roselaar 1995; Shirihai and Svensson 2018) and even the south-eastern Balkans (Keller et al. 2020; Roselaar 1995) as part of the breeding range of *samamisicus*.

The range of *samamisicus* certainly includes the Caucasus, which has been identified as an important Pleistocene glacial refugium for Palearctic passerines (Hung et al. 2017), and the two subspecies of Common Redstart might have evolved in different refugia, i.e., separated geographically (Hogner et al. 2012). However, no consistent phylogeographic structure in mitochondrial DNA (mtDNA) has

been identified across the species' entire range (Hogner et al. 2012). This potentially indicates that the subspecies are too young for differences to be reflected in mtDNA. However, two very different mtDNA haplogroups exist basically throughout the distribution of the Common Redstart, which could be the result of ancient isolation followed by secondary contact (Hogner et al. 2012). Whilst mtDNA might have been subject to introgression between the different populations, morphological differences could have been maintained via selection (Hogner et al. 2012).

Irrespective of the reasons for these patterns, thorough documentation of the morphological variation within Common Redstart across its range is not the only prerequisite to understanding its evolutionary history, but also identifying individual birds in the context of vagrancy. Common Redstarts with features apparently indicative of *samamisicus* sometimes are reported in western and northern Europe, but their identification and origin have proven controversial (cf. Shirihai and Svensson 2018; Small 2009).

One reason for contradictory statements in the literature concerning the prevalence and geographic location of introgression lies in the characters used to differentiate the two subspecies. Identification of females is at best tentative (based on the presence/indication of a pale wing panel and overall colder/greyer tones in *samamisicus*), whereas adult males are more readily identified by the presence (*samamisicus*) or absence (*phoenicurus*) of a large white wing patch formed by broad white fringes to the outer tertials, secondaries and, at least in fresh plumage, the primaries (Clement 2015; Shirihai and Svensson 2018; Small 2009). However, male Common Redstarts in their second calendar year retain juvenile primaries, secondaries and tertials until the post-breeding moult (Jenni and Winkler 2020), and individuals of *samamisicus* show much less white on the edges of these feathers (especially the tertials and secondaries) than in adults (Small 2009). Thus, second-calendar-year birds, particularly when the pale edges to the juvenile secondaries and tertials are abraded, can easily be misidentified as intergrades or even as the nominate subspecies. This potential pitfall was elucidated by Small (2009) but seems to have been largely ignored previously. For example, Stegmann (1928) and Cramp (1988) simply stated that white in the wing would also be present in juvenile and consequently in first-summer male *samamisicus*, overlooking that Hartert (1910) had already mentioned that young males may sometimes show only a hint of a white panel. Note, however, that this may well explain reports of sympatric breeding of *phoenicurus* and *samamisicus*, e.g., in the northern Caucasus (Serebrowski 1925, cited in Stegmann 1928), Armenia (Adamian and Klem 1999) and southern Bulgaria (Nikolov and Georgiev 2007). Another explanation for conflicting statements in the literature concerning intergradation between the two subspecies, already mentioned by Stegmann (1928), may be caused by *phoenicurus* migrating through the breeding range of *samamisicus*, with some migrants remaining late into the breeding season, at least compared to the earlier nesting local breeders.

In addition to differences in wing patch, males of both subspecies differ slightly in overall colour, with *samamisicus* being, on average, more intensely coloured than *phoenicurus*. This results in a darker mantle and a larger amount of black on the neck sides in *samamisicus* (Small 2009). Individuals of *samamisicus* with a black mantle have even been considered to represent a morph (named '*incognita*', e.g., Cramp 1988), and were originally described as a subspecies (Zarudny 1910).

Here, by applying a descriptive approach, we map the occurrence of the two different character states traditionally, and most reliably, used to separate males of the two subspecies of Common Redstart, i.e., of the wing patch and the coloration of the back, during the breeding season across the species' entire range. To this end, we took advantage of the availability of literally thousands of photos on the internet, found mainly in different citizen science databases, from virtually the entire breeding range. We tried to benefit from this unique dataset to analyse as many male Common Redstarts as possible, which was subsequently complemented by data from specimens held in various museums.

Methods

Character assessment

The main difference between male *samamisicus* and *phoenicurus* is the presence (*samamisicus*) or absence (*phoenicurus*) of a white wing patch (e.g., Shirihai and Svensson 2018; Small 2009). Based on an initial evaluation of variation in this character, we defined five character states ranging from an all-dark wing to a bold white wing patch (Table 1).

Some male *samamisicus* are characterized by a much darker mantle compared to the nominate form, or even a black mantle (the so-called '*incognita*' morph). To document the prevalence of this feature, we defined three character states for mantle coloration: (1) 'normal' dull blue-grey as in *phoenicurus*, (2) distinctly darker grey than *phoenicurus*, and (3) partially or completely black. It must be taken into account that grey shades can be difficult to assess on photographs without direct comparison under the same lighting conditions, thus we only scored as (2) those individuals that were obviously dark grey.

If possible, birds were aged based on moult contrast in the greater coverts and/or moult contrast between the wing feathers and mantle (Jenni and Winkler 2020; Svensson 1992). Ageing was performed mainly by NM but cross-checked by MS and by an experienced bird ringer (Fabian

Table 1 Scores corresponding to numbers for different character states for analysing the extent of the white wing patch

●	1: no white/whitish wing patch; including birds with (more or less prominent) buff or grey margins to the secondaries (and primaries) creating a buff/grey wing patch (sometimes rather pale grey, but never white or whitish)
●	2: very narrow whitish (not pure white) margins to the secondaries, which do not create the impression of a patch even on the closed wing (either because the dark parts are still visible between the whitish, or the wing patch is pale grey)
●	3: narrow pure white fringes to the secondaries (and primaries) creating a (narrow) white wing patch at certain angles
●	4: rather broad pure white margins on the secondaries creating a clean white and obvious wing patch; primaries without (obvious) white
○	5: broad pure white margins on the secondaries incl. tertials 2–3 creating a clean white and obvious wing patch; primaries also with white margins

Schneider). Cross-checking was performed on a random sample of 100 birds plus all non-adult birds from the breeding areas of *samamisicus* (based on the results reported herein) and many supposed second calendar year (hereafter 2cy) males from the Balkans and Ukraine, as any errors in these regions would potentially have the greatest impact on the results.

All scoring was performed by the same person (NM) to achieve maximum consistency, but a random sample of 100 birds was cross-checked by MS. Mean difference was 0.05 scoring points and differences never exceeded 1 scoring point.

Data collection and analyses

To document plumage variation of male Common Redstarts during the breeding season across the species' entire range, we searched for photographs on the internet, mainly on various citizen science databases (for a list of these, see Table S1). We considered only (i) photographs of birds that were obviously nesting (e.g., carrying food, copulating) or (ii) were taken between 15 May and 31 July, as these dates cover the species' main breeding period (Glutz von Blotzheim 1988). Moreover, the migration of nominate birds through the breeding range of *samamisicus* should be effectively over by mid May (Handrinos and Akriotis 1997; Kirwan et al. 2008).

If multiple photos from a single site (i.e., the environs of a village) in the same year were available they counted as one bird, unless it was obvious that more than just one individual was involved. As we were mainly interested in the pattern of the wing (see before), only those photographs which permitted wing coloration/pattern to be critically assessed were considered.

Secondly, we consulted a number of museum collections, particularly to further enhance our sample from regions of potential introgression between the two subspecies of Common Redstart identified from the initial analysis of internet photographs, but also to confirm or refute patterns evident from the latter using material that is easier to categorise and reliably score using the characters selected. To this end, GMK photographed all relevant material (based on the dating parameter [ii] mentioned above) at the following museums (with acronyms and numbers of specimens eventually used for this study in parentheses): Natural History Museum, Tring (NHMUK, $n = 11$); Museum für Naturkunde, Berlin (ZMB, $n = 8$); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK, $n = 10$); and Museum of Zoology, University of Cambridge, UK (MZUC, $n = 3$). Among the material examined, but not analysed, for this study, was the type of *Sylvia mesoleuca* Ehrenberg, 1833, taken on spring migration in Jeddah, Saudi Arabia (at ZMB), which name is a synonym of *Motacilla samamisica* Hablizl, 1783 (= *P. p. samamisicus*). Furthermore, MS checked specimens in the Naturhistorisches Museum, Bern (NMBE, $n = 2$). In addition, photos of relevant specimens (fulfilling category [ii] above and originating from regions with scant material in citizen science databases and of specific interest, i.e., suspected intergradation zones, the main range of *samamisicus*, Central Asia, and North Africa) were solicited and received from the following museums (alphabetical order): American Museum of Natural History, New York (AMNH, $n = 5$); Field Museum of Natural History, Chicago (FMNH, $n = 2$); Museum of Comparative Zoology, Cambridge, MA (MCZ, $n = 2$), Manchester Museum (MM, $n = 1$); Slovenian Museum of Natural History, Ljubljana (ML, $n = 1$); National Museum of Natural History, Bulgarian Academy of Sciences, Sofia (NMNHS, $n = 2$); Natural History Museum, Belgrade (NHMBEO, $n = 2$); the Naturalis Biodiversity Center, Leiden (RMNH, $n = 2$); Darwin State Museum, Moscow (SDM, $n = 13$); University of Michigan Museum of Zoology (UMMZ, $n = 1$); University of Washington Burke Museum (UWBM, $n = 4$); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM, $n = 7$); Biodiversity Research and Teaching Collections (TCWC, $n = 2$); Museum für Naturkunde Berlin (ZMB, $n = 8$); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZMFK, $n = 14$). Replies were received from four additional museums, confirming that they had no male specimens collected during the key mid May to end of July period and the above-mentioned regions: Muséum national d'Histoire naturelle, Paris (MNHN); Naturhistorisches

Museum, Basel (NMBA); Yale Peabody Museum (YPM) and Zoological Museum, University of Athens (ZMUA).

In order to analyse frequencies of different wing scores and back colour, the following regions were used: Central Asia (Afghanistan, Pakistan, Tajikistan, Turkmenistan, Uzbekistan, Kyrgyzstan, southeastern Kazakhstan), Northern Asia (Siberia, Mongolia, China, northeastern Kazakhstan); Fennoscandia (Denmark, Finland, Norway, Sweden); European Russia and western Kazakhstan; Central Europe and UK (United Kingdom and countries from continental Europe including northern Ukraine, Italy north of Genoa, cf. Martinez and Martin 2020); Iberia and North Africa (Algeria, Morocco, Portugal, Spain, Tunisia); Italy south of Genoa; Croatia and Slovenia; the Balkans (Albania, Bosnia and Herzegovina, northern Bulgaria, Kosovo, Montenegro, southern and coastal Romania, Serbia); coastal Ukraine and Rostov Oblast, Russia; Crimea; Greece and southern Bulgaria; western Turkey; eastern Turkey; northern Caucasus (northern Azerbaijan, Georgia, Russian Caucasus), *samamisicus* core range (Armenia, southern Azerbaijan, Iran).

Results

Wing patch score

We analysed photos of a total of 1072 males (including 80 museum specimens) from the period 15 May−31 July and certain breeders on unknown dates or photographed on earlier dates ($n = 62$). Of these, 588 were aged as adults (55%, including 41 museum specimens) and 346 as 2cy birds (among them 33 museum specimens), whilst ageing was not possible for the remaining 138 individuals (including five museum specimens). Birds with the most extensive white wing patches (= score 5) pertaining to the phenotype of *samamisicus* were found exclusively in Greece, southern Bulgaria, all of Turkey, Crimea, the Caucasus, Armenia, southern Azerbaijan and Iran (Figs. 1, 2).

Birds with rather broad pure white margins on the secondaries creating a clean white and obvious wing patch (= score 4), and those with narrow white edges (= score 3) were recorded across the entire breeding range of the species. However, the proportion of such birds clearly decreased with increasing distance from the areas where birds with a score of 5 were recorded (see above). Whitish margins on the flight feathers (= score 2), however, were also commonly observed in the region traditionally assigned to *phoenicurus* (i.e., Maghreb, most of Europe, Asian part of Russia, Kazakhstan, north-western China and Mongolia), with approximately 10−15% of all birds analysed in these regions scored thus.

The proportion of pale-winged birds (= scores 2−4) remained virtually unchanged in the range traditionally assigned to *phoenicurus* (see above) when unaged and 2cy birds were excluded (Figs. 1b, 2). On the other hand, no adults without obvious wing patches (< score 4) were recorded in Greece, southern Bulgaria, all of Turkey, Crimea, the Caucasus, Armenia, southern Azerbaijan and Iran. However, when males of all ages were included, the full range of character scores for the wing was identified in these same areas (Figs. 1a, 2).

Mean values of wing patch scores for different regions confirm these findings (Fig. 3). Intermediate values were observed in the Balkans, southern Ukraine, and Rostov Oblast (southern Russia) and, to a much lesser extent, this is also true for southern Italy, Iberia and north-west Africa.

Darkness of mantle

Males with a black or blackish mantle were observed in Greece, southern Bulgaria, much of Turkey, Crimea, the Caucasus, Armenia, southern Azerbaijan and Iran (Fig. 4). The proportion of such birds was highest in Turkey (especially in the west and south of the country) and Iran and rather low in the Russian Caucasus, Azerbaijan, Greece and Bulgaria (cf. Figs. 4, 5). In general, mantle coloration appears to be a very variable feature in this area.

Discussion

Geographic variation

Our results confirm that a complete white patch in the wing (score 5) or a lack of any white in the wing (score 1) are just extremes of a rather variable feature in adult male Common Redstarts. Previously, the absence/presence of a white wing patch in adult males was often considered to be the principal single feature separating the subspecies *samamisicus* from nominate *phoenicurus* (Clement 2015; Cramp 1988). However, as has been already indicated (e.g., Shirihai and Svensson 2018; Small 2009), this is not sufficiently precise for identification given that adult male Common Redstarts with some white in the wing can be found across almost the entire range of the species. Nevertheless, variation in this feature is strongly geographically structured and no adult males with a wing score < 4 were found during the breeding period in Greece, southern Bulgaria, all of Turkey, Crimea, the Caucasus, Armenia, southern Azerbaijan and Iran. This region should be considered as the breeding range of *samamisicus*. This hypothesis is supported by birds with a blackish mantle, a feature usually associated with *samamisicus*, being restricted to the same geographical region in our dataset. Contra Cramp (1988), birds with a mainly black mantle were not restricted to the eastern part of the range of *samamisicus*, and as birds with an all-black mantle represent

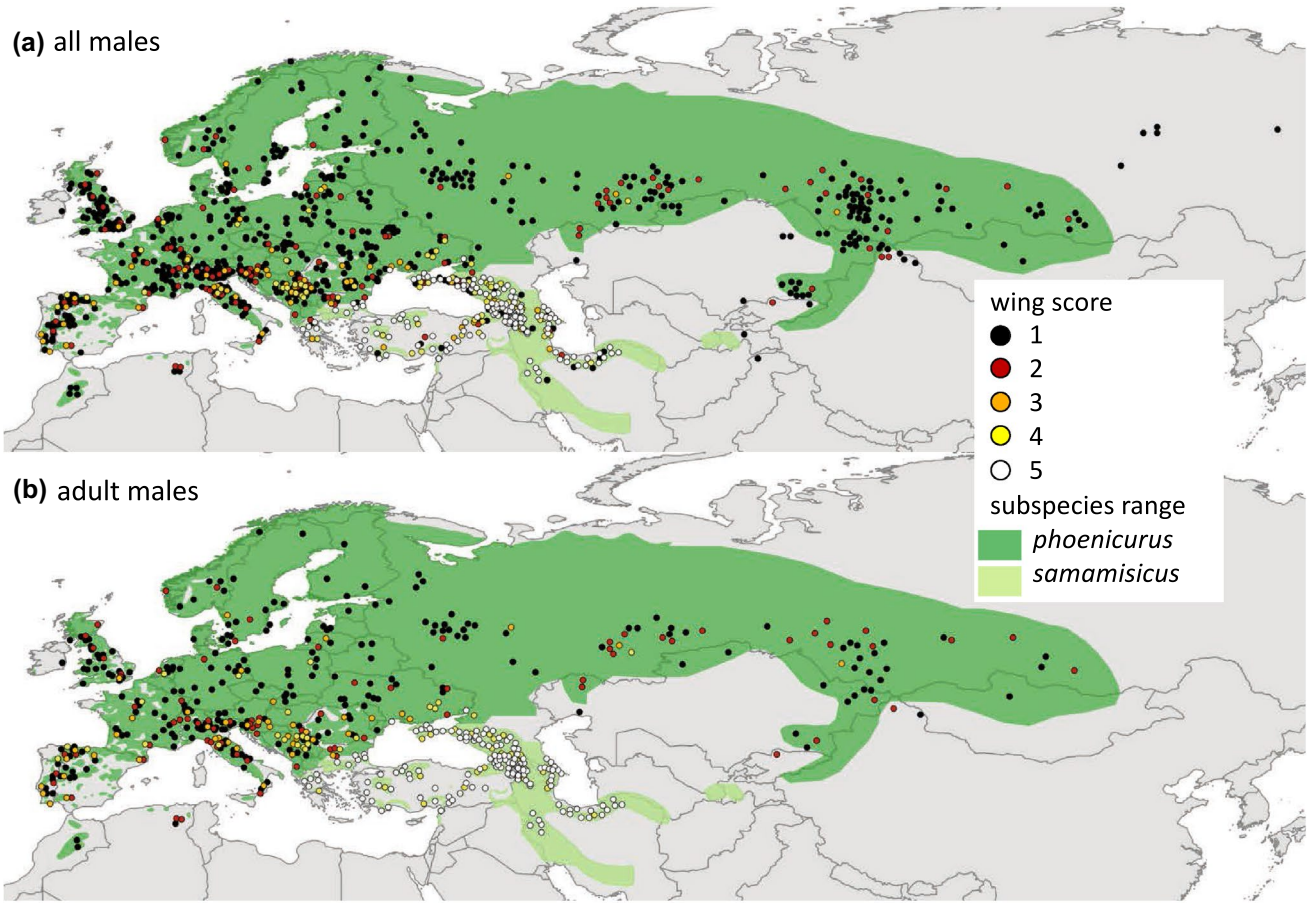

Fig. 1 Wing patch variation across the breeding range of Common Redstart *Phoenicurus phoenicurus* (cf. Table 1) with **a** showing the results when photos of males of all ages are mapped, whereas in **b** only adult males are plotted. Each marker corresponds to an individual. Where markers overlapped each other, we shifted points slightly to maximise their visibility. Map sources: www.birdlife.com (species' breeding range) and Natural Earth (www.naturalearthdata.com, countries). Subspecies distributions (*phoenicurus* green, *samamisicus* pale green) are based on the results reported herein (color figure online)

only the extreme of a rather broad variation, recognition of this phenotype as a morph is not warranted (Figs. 6, 7, 8, 9).

When 2cy year birds were also considered, a significant proportion of males showed character scores < 4 in the range of *samamisicus* as defined above. Thus, reports of intermediates and/or *phoenicurus* breeding in the northern Caucasus (Stegmann 1928) probably reflect confusion with 2cy male *samamisicus*. This might also be the case for various sources mentioning Turkey as a zone of intergradation (e.g., Svensson 1992; Vaurie 1959) and, additionally, late migrating individuals of *phoenicurus* might have further engendered confusion. Moreover, from our survey of photographs and specimens we have no indication that *phoenicurus* or intermediates might breed in Greece or southern Bulgaria, contra Handrinos and Akriotis (1997) and Nikolov and Georgiev (2007).

Our results document the existence of two areas where considerable variation in wing scores between the extremes can be found, namely coastal Ukraine and the Rostov Oblast, with a high proportion of scores 2−5, and parts of the Balkans (Bosnia and Herzegovina, northern Bulgaria, Kosovo, Montenegro, southern Romania and Serbia), with a large percentage of scores 1−4 (examples see Fig. 9). We consider these areas as pertaining to more or less broad zones of intergradation between *samamisicus* and *phoenicurus*. The existence of a zone of intergradation in parts of the Balkans was already mentioned by Matvejev and Vasić (1973) for Kosovo, North Macedonia and Serbia, indicating that it might have been stable for some decades (or longer). An adult male from 1 July 1949 collected in Kopaonik National Park (southern Serbia) held at NHMBEO with a wing score of 4 offers support for this hypothesis. On the other hand, intergradation in northern Bulgaria might be of more recent origin given the species' marked increase in breeding range at least in southern Bulgaria (Milchev 2010).

Similarly, the intergradation zone north of the Black Sea, north and west of Crimea (i.e., coastal Ukraine and Rostov Oblast), might have become established quite

Fig. 2 Proportions of male Common Redstarts *Phoenicurus phoenicurus* with wing scores 1−5 in different regions. Upper graph: all males ($n = 1072$), lower graph: only adult males ($n = 588$) (color figure online)

recently. Southern parts of Ukraine were colonised only in the second half of the twentieth century and Tsvelykh (2013) recently postulated that a contact zone could form in the near future as a result of birds simultaneously colonising the area from the south (*samamisicus*, Crimea) and the north (*phoenicurus*, northern Ukraine). Our results indicate that this has indeed already occurred, but given the presence of birds with intermediate characters well east of the Crimea, between Mariupol, Ukraine, and Rostov on Don, Russia, it seems likely that *samamisicus* colonised southern Ukraine from the western Caucasus, too. Unfortunately, we had only scant material from Russia north of the Caucasus, however, Glutz von Blotzheim (1988) mentioned the presence of intergrades in the Kuma–Manych Depression.

The absence of wing scores < 4 from Greece and Crimea south-eastwards, in contrast to the presence of adult males with a wing score of 4 basically throughout the species' range might indicate asymmetric introgression from *samamisicus* into *phoenicurus*. However, this possibility requires further investigation and a certain amount of white in the wing in *phoenicurus* might simply be part of this subspecies' natural variation. Adults with whitish or narrow white fringes on the secondaries appear to be marginally more numerous in Iberia and North Africa compared to the rest of the breeding range of *phoenicurus*. This is in line with Kleinschmidt (1904) who reported that birds from Algeria can have a more obvious white wing patch than individuals of the nominate subspecies in Europe and named them *Erithacus algeriensis* (now a synonym of *P. p. phoenicurus*)

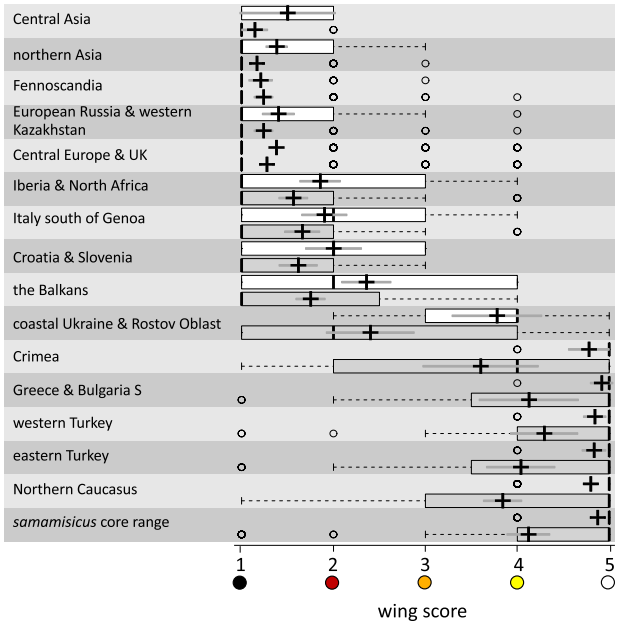

Fig. 3 Extent of white wing patch in male Common Redstarts *Phoenicurus phoenicurus* by region (boxplot including mean value (+), 83% confidence interval (grey line), lower and upper quartile (boxes), Tukey whiskers (dashed lines, highest and lowest values excluding outliers) and outliers (dots), for all males (grey, $n = 1072$) and only adult males (white, $n = 588$) (color figure online)

on the basis of four males held at ZFMK. Note, however, that these four males (three adults, one 2cy male) formed part of our sample and do not show above average amounts of white in the wing for *phoenicurus* (one adult was scored 1, and the others two were scored 2). The comparatively large percentage of birds with pale wing patches (mainly score 3) also in Italy is interesting in the context of the widespread occurrence in this country of a call variant that is otherwise typical of *samamisicus* (Martinez and Martin 2020). Future studies will be necessary to investigate if this can be interpreted as evidence of introgression from *samamisicus* or is reflective of geographic variation independent of gene flow from the latter.

Our results and their interpretations are strongly dependent on accurate ageing. Therefore, ageing was cross-checked for many birds independently, including all supposed 2cy *samamisicus*. However, differences between regions remain discernible when all males are included, with still a minority of birds displaying wing-scores < 4 in the range of *samamisicus*.

Identification of subspecies away from the breeding grounds

The existence of broad zones of intergradation combined with the existence of *phoenicurus* with more or less

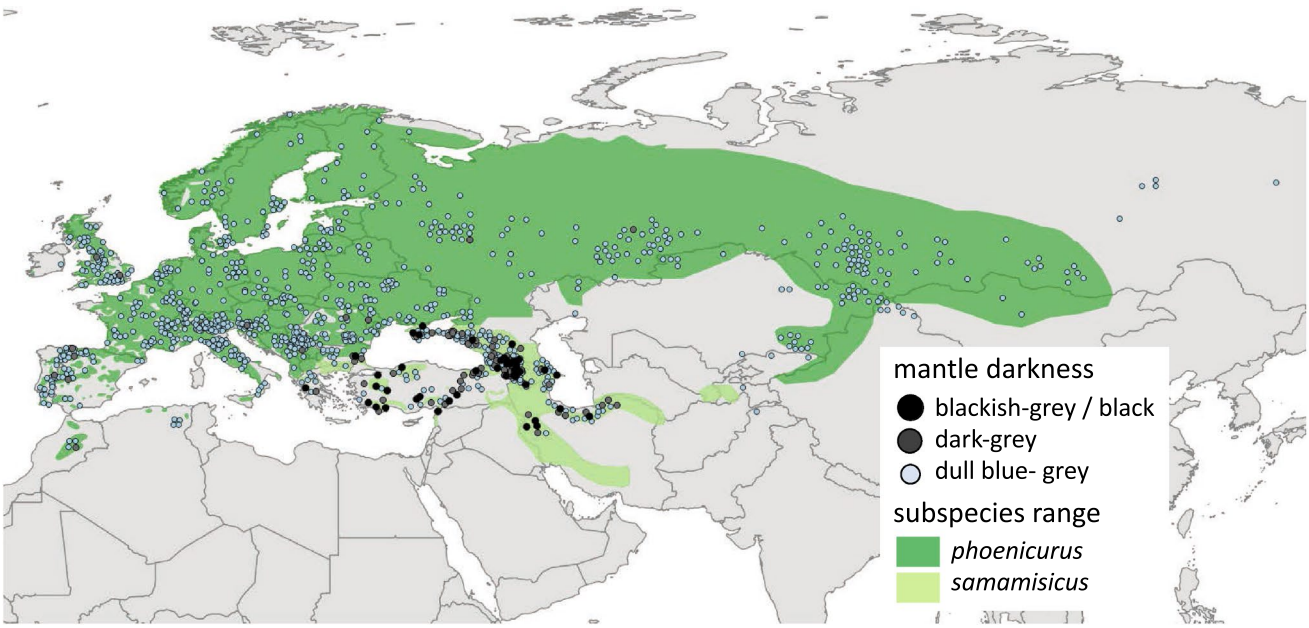

Fig. 4 Variation in mantle darkness in males across the breeding range of Common Redstart *Phoenicurus phoenicurus*. Each marker corresponds to an individual. If markers overlapped each other, we shifted points slightly to maximise their visibility. Map sources: www.birdlife.com (species' breeding range) and Natural Earth (http://www.naturalearthdata.com, countries). Subspecies distributions are based on the results reported herein (color figure online)

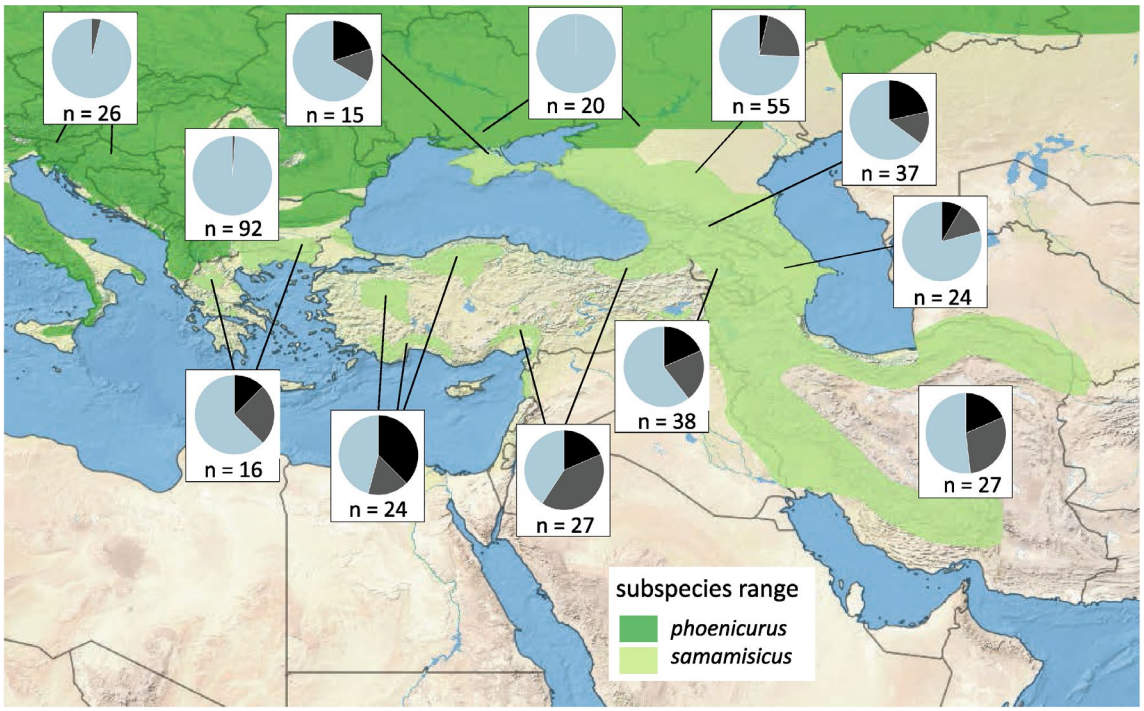

Fig. 5 Proportion of males with a blackish-grey or black (='*incognita*', black), dark-grey (dark-grey) and normal-patterned (dull blue-grey) mantle in the range of *samamisicus* and immediately adjacent countries. Map sources: www.birdlife.com (breeding range) and Natural Earth (www.naturalearthdata.com, background, countries). Subspecies distributions are based on the results reported herein (color figure online)

prominent white wing patches makes the identification of vagrant *samamisicus* a real challenge. Based on our results, only adult males with a wing score of 5, or those with a wing score of 4 and additionally displaying an at least partially black mantle can be safely identified as *samamisicus* away from the subspecies' breeding grounds. However, it must be taken into account that *phoenicurus* can exhibit a rather dark mantle, especially in strongly abraded plumage. We concur with Small (2009) that 2cy *samamisicus* are not safely identifiable in the field, but would further suggest that even the large majority of 2cy birds in the hand should be left unidentified due to the prevalence of a broad intergradation zone, with birds displaying intermediate characters, and the presence of such birds well away from the breeding grounds of *samamisicus*. An exception are birds that already show large white parts on several wing feathers reminiscent of adult *samamisicus*, either through natural variation or accidental replacement of juvenile feathers.

Consequently, a significant percentage of male *samamisicus* cannot be safely identified in a vagrant context in spring. Note that we examined adults in worn summer plumage and the situation in autumn might prove to be even more complex as (white) fringes to fresh feathers at this season would be generally broader and more striking not only in *samamisicus*, but also in *phoenicurus* and intergrades, thereby complicating identification even further.

A constant *heed* call might certainly offer a supportive character for *samamisicus*, however, birds breeding well away from the range of *samamisicus*, e.g., on the Italian peninsula and in eastern Siberia, can sound identical (Martinez and Martin 2020). Given that there is no consistent phylogeographic structure in mitochondrial DNA and two very different mtDNA haplogroups exist throughout the species' range (Hogner et al. 2012), simple mtDNA barcoding is of no assistance.

Citizen science data vs. museum specimens

In this study, we made significant use of well-labelled photographs archived on publicly available citizen science databases on the internet. This enabled us to acquire a much larger and geographically more comprehensive dataset than would have been available using museum specimens alone. Even if we had been able to include more data from additional natural history collections, given our closely defined temporal (date) and sex-related parameters, we would have been unable to assemble a similar dataset using museum specimens alone. For example, NHMUK has hundreds of specimens of Common Redstart, but after one has

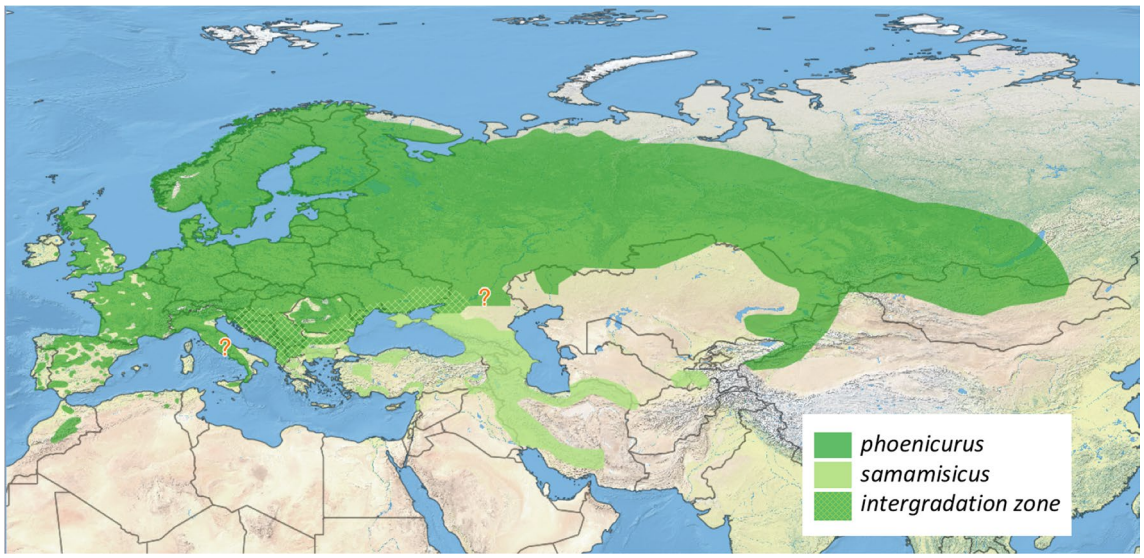

Fig. 6 Proposed subspecies' ranges in the Common Redstart *Phoenicurus phoenicurus* including intergradation zones. Map sources: www.birdlife.com (breeding range) and Natural Earth (www.naturalearthdata.com, background, countries) (color figure online)

Fig. 7 Typical adult male of *samamisicus* (score 5, 24.04. 2011, Georgia, NM, left) with grey back, one with a blackish back (score 5, but white on primaries less visible, 29.05.2010, Bursa, northwestern Turkey, E. Üç, middle) and typical adult male *phoenicurus* (score 1, 26.5.20, Switzerland, NM, right) (color figure online)

Fig. 8 Typical adult male *samamisicus* (score 5, 25.5.2009, K. Gaugner) showing well the exact pattern on the wing. Note that many *samamisicus* have no white on T1, unlike this bird (color figure online)

discounted all of those that are females or collected outside the 2.5-month period of interest to us, the number of individuals available for analysis shrunk to fewer than 15! As the precise wing pattern was not always easy to interpret from photographs taken in the field, museum specimens were useful to corroborate our results. However, we would stress that whilst scoring wing patterns in Common Redstart can often be more or less straightforward from photographs, analysing subtle colour hues is more difficult and, of course, absolute measurements can never be taken from such sources. Moreover, additional morphological and anatomical information, as well as DNA, can be analysed from museum specimens (Raxworthy and Smith 2021; Webster 2017). Furthermore, the long-term availability of citizen science databases on the internet is not always guaranteed, thereby potentially limiting the reproducibility of studies based on such data. As a

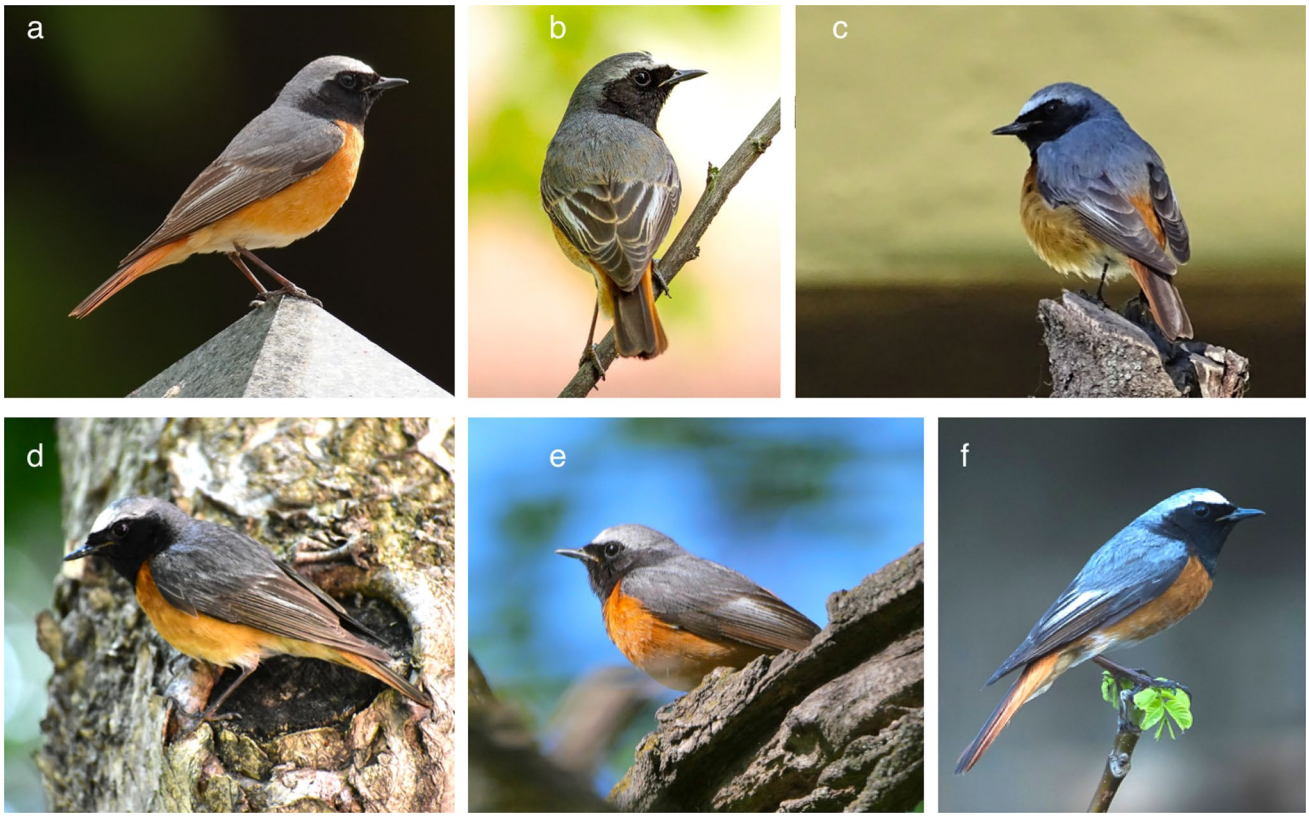

Fig. 9 Adult males from **a** Croatia (score 3, 8.5.2019, S. Ascic), **b** Cherson, Bosnia (score 4, May, N. Sokol), **c** Bucharest, Romania (score 4; 18.5.2021, I. Anania), **d** south-western Ukraine (score 3, 9.6.21, biowithmi*), **e** Mariupol, south-eastern Ukraine (score 4, 5.5.2020, O. Prysiazhniuk), **f** Dnipro, south-eastern Ukraine (score 4, 19.5.2019, V. Kaistro). * https://www.inaturalist.org/observations/82291911, https://creativecommons.org/licenses/by-nc/4.0/

result, museum collections possess invaluable advantages over photographs deposited on citizen science databases and the latter will consequently never serve as a complete substitute for the former. However, our approach of combining museums with numerically more numerous citizen science data, and thereby benefiting from the advantages offered by both, might serve other similar investigations well.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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