

Redstart hybrids in Europe and North Africa

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Abstract An analysis of 121 wild Black Redstart *Phoenicurus ochruros* x Common Redstart *P. phoenicurus* hybrids from Europe and North Africa is presented, with an overview of distribution, phenology, habitat, biometrics, phenotypes and vocalisations. Records of hybrid redstarts have increased markedly over the past 30 years. Such birds show an intermediate phenology but in terms of habitat choice are more similar to Black Redstarts. No wild female hybrids were found, which must be related to reduced detectability. The locally more abundant species usually plays the role of the female in mixed pairs and in pairs with male hybrids. Plumage variation within male hybrids is higher than previously documented. Primary spacing ratio and the presence of emarginations on P6 are useful identification features for hybrids, but there is substantial overlap with both parental species, and with ‘Eastern Black Redstart’, especially *P. o. phoenicuroides*. Song of hybrids may approach Black Redstart in structure and presence of the ‘scratchy’ part, but matches Common Redstart in pace and strophe length.

Introduction

In Europe, Black Redstarts *Phoenicurus ochruros gibraltariensis* and nominate Common Redstarts *P. p. phoenicurus* (hereafter *gibraltariensis* and *phoenicurus* respectively) originally occupied different habitats: *gibraltariensis* bred in alpine regions and *phoenicurus* in wooded habitats, and contact zones were restricted to the upper tree line. However, when both species began to colonise human settlements, a secondary contact zone emerged (Ertan 2002): *gibraltariensis* occupied buildings as an alternative to rocky areas, while *phoenicurus* settled in orchards, villages and parks. This probably resulted in an increase in hybridisation (Ertan 2002). Niche separation in urban environments was studied by Grosch (2003, 2004) and Sedláček *et al.* (2004), and the former carried out experiments with hybrids and backcrosses. Others investigated the genetic component of migratory behaviour (*gibraltariensis* is a short-distance migrant while *phoenicurus* is a long-distance migrant) and showed that hybrids exhibit intermediate

migratory behaviour, at least in captivity (Berthold & Querner 1995; Berthold *et al.* 1996).

Natural (= wild) redstart hybrids were first described by Kleinschmidt (1907/08) and Heim de Balsac (1929); Droz (2011) gave a recent overview, describing 39 hybrids. Male hybrids share many similarities with ‘Eastern Black Redstart’, especially the rufous-bellied form *P. o. phoenicuroides* that breeds in Central Asia and has occurred as a vagrant to Europe (Ebels *et al.* 2018), prompting identification papers such as Nicolai *et al.* (1996), Lindholm (2001), Steijn (2005), Petersson *et al.* (2014), Stoddart (2016) and van der Spek & Martinez (2018). Box 1 presents an overview of the separation of hybrids and Eastern Black Redstarts.

Based on 121 redstart hybrids from Europe and North Africa, we present an overview that covers variation in phenotypes, distribution, phenology, vocalisations and analyses of mixed pairs; to our knowledge, this is the most extensive work on natural redstart hybrids.

Methods

Data collection

We searched for records of redstart hybrids and mixed broods in published literature and online. Additional observations were collected from direct contacts and online searches (the following internet platforms were searched systematically: www.waarneming.nl, www.waarnemingen.be, www.netfugl.dk, www.observation.org, www.xeno-canto.org, www.tarsiger.com and national/regional ornitho-platforms from Austria, Catalunya, France, Germany and Switzerland). For each hybrid claim, we collected all available information on phenotype, arrival date, breeding, song and call, including recordings and images. In many cases we contacted observers directly, for more specific information. References to all analysed birds and additional photographs can be found at <https://bebbibabblers.jimdo.com/projekte/rotschwanz-hybriden>. For the analysis of 'mixed singers' we searched www.ornitho.ch only and combined the results with our own and published observations. Mixed singers were defined as birds that resemble classic male *phoenicurus* in appearance but regularly give *gibraltariensis*

song. Note that in Common Redstart song the final flourish consists of mimicry and this can include Black Redstart song. Mixed singers differ by copying complete strophes. Seemingly classic-looking *gibraltariensis* that regularly give *phoenicurus* song were not found.

Analyses

Potential hybrids were classified based on available descriptions, images and/or measurements and assigned to one of the following categories: 1 = confirmed hybrid (wing measurements); 2 = confirmed hybrid (images); 3 = confirmed hybrid (description and/or earlier publication); 4 = unconfirmed hybrid (claims without description or images; also records of Eastern Black Redstarts not accepted by national rarity committees when a hybrid was considered the more likely option); 5 = hybrid or 'red-bellied' *gibraltariensis*; 6 = 'red-bellied' *gibraltariensis* (birds with extensive red on the underparts that otherwise have characters only of *gibraltariensis*). Whenever possible, photographed birds were aged by the presence/absence of moult limits and adult-type greater-coverts.



D. Kratzer

III. Male hybrid Black Redstart *Phoenicurus ochrurus* x Common Redstart *P. phoenicurus* (foreground) with male Black Redstart *P. o. gibraltariensis*, Wyhlen, Germany, 31st March 2012. This hybrid was seen in a flock of no fewer than 153 *gibraltariensis*. It can be separated from 'Eastern Black Redstart' *P. o. phoenicuroides* by (for example) the white undertail-coverts, a shallow dark breast-patch and a large white belly-patch.

To assess differences in phenology, we compared arrival dates (first sighting date) of both parental species from Germany (from www.ornitho.de accessed in August 2017) with those of hybrids from the Benelux countries, Germany and Switzerland. We used hybrids from these countries only because they are from a similar geographical area. We assessed the breeding habitat for each territorial hybrid and mixed singer and assigned these to seven different categories. Based on available information on habitat choice (Cramp 1988; Glutz von Blotzheim & Bauer 1988) and our own experience, we compared the habitat of hybrids and mixed singers with that of both parental species.

Only photographed birds were used to analyse plumage variation. Using a set of pre-defined criteria (table 2), six main plumage types were identified. Nearly 100 hybrids were bred in the 1990s by Peter Berthold's group (Vogelwarte Radolfzell), with interesting results on genetics (Ertan 2002, 2006), migration (Berthold *et al.* 1996; Berthold 2001), habitat selection, and foraging behaviour (Grosch 2000, 2003, 2004). To our knowledge, there are no detailed studies on morphology and plumage, although some relevant information is given in Grosch (2000), Ertan (2002) and Steijn (2005). In 2011–12, seven captive-bred hybrids (four males, two females and one female F2 hybrid) were transferred to Museum Heineanum in Halberstadt. As they had been kept in aviaries and their bodies then stored in freezers, their condition is not perfect, but since their parental origin was known, these birds provided valuable additional informa-

tion on plumage features. Grosch (2000) and Ertan (2002) collected biometric data; we combined these with data from wild hybrids.

For many singing hybrids and mixed singers, short descriptions of the song were available. To a much lesser extent this was also true for calls. Wherever possible, for both song and calls, we assigned each bird to one of the following five categories: similar to *gibraltariensis*; similar to *phoenicurus*; mixture of both species; both species alternately; and atypical vocalisations. For a few hybrids and mixed singers, recordings were available. These were analysed with Raven Lite and the number of song strophes according to the five categories above were noted. For complete *gibraltariensis* strophes, the total length and the length of the pause before the scratchy part was measured and compared with strophes of pure *gibraltariensis*. We defined complete *gibraltariensis* strophes as those starting with some clear notes that may form a trill, followed by a pause, continued with a scratchy part and ending with a couple of trills. Note that the scratchy part can be replaced by heavily modulated trills.

Results

Temporal and geographical occurrence

Reports of hybrids were rare until 1990, but then increased strongly (fig. 1). For this study, we used observations of 121 hybrid males (categories 1–3, table 2): 30 confirmed by biometrics, 48 by photographs and 43 described and/or from previous publications (without images). Four poorly marked birds, still clearly identifiable as males, were

observed in autumn and may have been 1CY birds. We found no confirmed wild female hybrids (but see captive hybrids, below).

Redstart hybrids have been observed across Europe, in at least 16 countries. Records are especially numerous in Germany (47 birds), Switzerland (17), France (8), the Netherlands (8) and Sweden (8). There

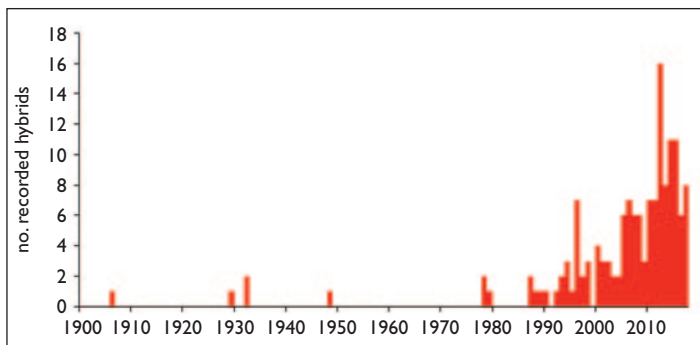


Fig. 1. Number of Black Redstart *Phoenicurus ochrurus* × Common Redstart *P. phoenicurus* hybrids recorded annually in Europe and North Africa, 1900–2017 ($n=121$).

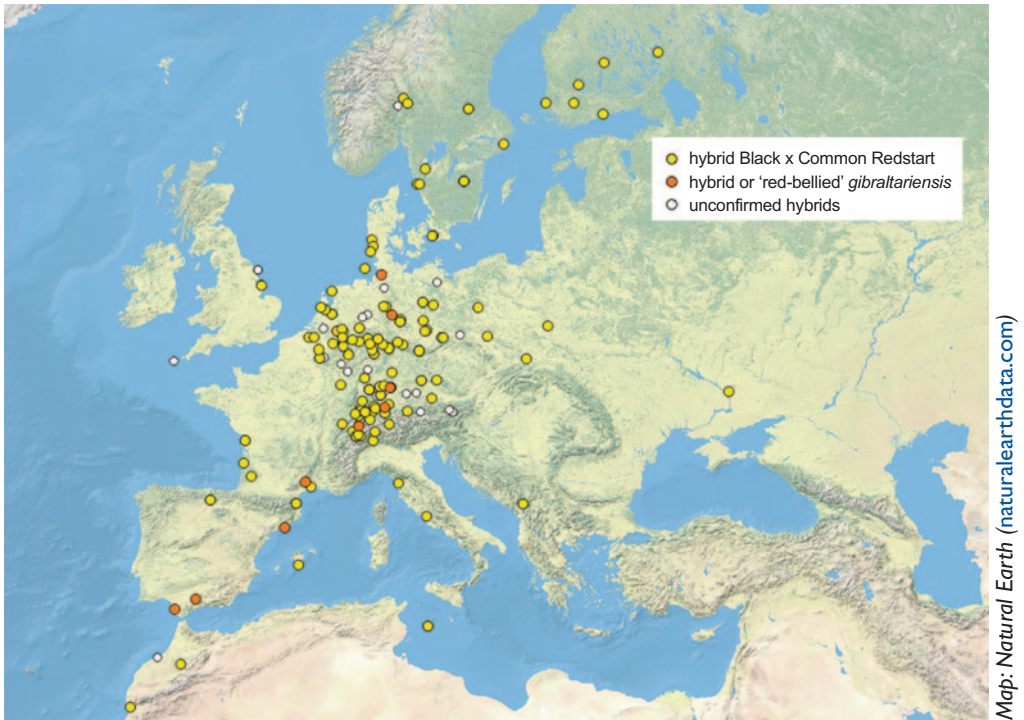


Fig. 2. Records of Black Redstart x Common Redstart hybrids in Europe (yellow dots; n=121), plus seven records of birds that are either hybrids or ‘red-bellied’ *P. o. gibraltariensis* (orange) and an additional 31 sightings of unconfirmed hybrids (white).

are relatively few records from southern Europe: Italy (6), Spain (2) and Albania (1, Ernst 2017). One in Ukraine in 2014 (Fesenko & Shybanov 2016) is the only record east of Poland (3) and south of Fennoscandia (fig. 2). Two records from Morocco are the only confirmed hybrids from North Africa (Demey 2009; Robel & Nicolai 2009).

Mixed pairs and breeding hybrids

We found 29 mixed *gibraltariensis* and *phoenicurus* pairs, of which at least 18 bred. Seventeen pairs were formed by a *phoenicurus* male and a *gibraltariensis* female, and 12 pairs were composed of a *phoenicurus* female and a *gibraltariensis* male. Of the 17 which involved *phoenicurus* males, five (29%) males were mixed singers and one performed a typical *phoenicurus* song (see vocalisations section, below); no information was available for the remaining 11 males. There was a clear difference between Fennoscandia and central Europe in the composition of the pairs. All seven mixed pairs from Fennoscandia were formed by a male *gibraltariensis* and a female

phoenicurus, while in central Europe 17 of the 22 mixed pairs (77%) comprised a male *phoenicurus* and a female *gibraltariensis*.

Hybrid males also breed. Of 34 breeding attempts by male hybrids with (assumed) pure females (of either species), two pairs abandoned their nests before laying. Of the remaining 32 pairs, at least 20 were successful: 24 pairs comprised a hybrid male and a *gibraltariensis* female (75%), and eight pairs a hybrid male and a *phoenicurus* female (25%). Again, all hybrids from Fennoscandia were paired with *phoenicurus* females (five pairs), whereas most hybrids from central Europe were paired with *gibraltariensis* females (24 of 27 pairs, 89%).

Phenology of hybrids and parental species

In Europe, hybrids are most often detected in spring: 82% of all records occur between mid March and late June, with a much smaller autumn peak in September and October (fig. 3). The earliest observation of a certain hybrid in Europe is 7th March 1997, in Rome, Italy (Bulgarini & Fraticelli 1998); the

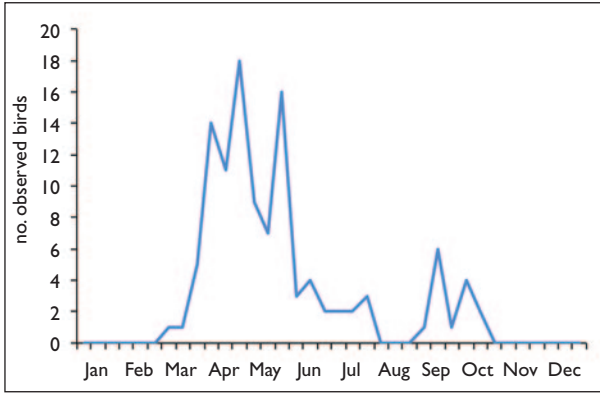


Fig. 3. Timing of hybrid Black Redstart x Common Redstart sightings in Europe (n=112). Nine returning birds were counted for each year they were seen, of which five birds returned once, and four returned twice.

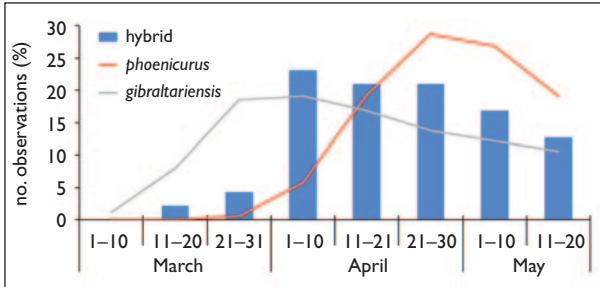


Fig. 4. Spring phenology of Black Redstart x Common Redstart hybrids (blue, n=48) in Germany, Switzerland and the Benelux countries compared with *gibraltariensis* (grey, 97,165 observations) and *phoenicurus* (orange, 51,392 observations) in Germany (data from www.ornitho.de for both species). Returning hybrids were counted for each year they appeared.

(ringed at Subigerberg, Switzerland; T. Lüthi *in litt.*), 8th October 2008 (photographed at Cap Ferret, France; L. Barbaro, www.faune-aquitaine.org) and 12th October 2012 (ringed and photographed on Lampedusa, Italy; G. Papale *in litt.*).

Records of hybrids from Germany, Switzerland and the Benelux countries (n=48) suggest that their phenology in spring falls in between the peak of the two parental species. Hybrids peak around 1st–10th April, while *gibraltariensis* peak between 21st March and 10th April and *phoenicurus* 21st–30th April (fig. 4).

Habitat

The majority of the territorial male hybrids were present in anthropogenic habitats, where *gibraltariensis* is typically abundant (mainly in villages and dense human settlements) but where *phoenicurus* occurs too (table 1). Significant numbers were also found in dense human settlements with few green areas, as well as in city centres and similar habitats lacking green areas or trees. Only a minority of hybrids were observed in typical ‘*phoenicurus*-only’ habitats. Mixed singers occur in approximately similar habitats.

latest records of confirmed hybrids from mainland Europe are 8th October 1993

Table 1. Habitat of territorial Black Redstart x Common Redstart hybrids (n=54) and mixed singers (n=19) compared with habitat choice of *P. o. gibraltariensis* and *P. phoenicurus*. Key: – mostly absent or very rare, + rare, ++ local, +++ abundant.

habitat	<i>gibraltariensis</i>	hybrid (%)	mixed singer (%)	<i>phoenicurus</i>
forest, forest margin	–	11	11	+++
orchard	–	0	11	+++
open landscape with single buildings, urban green zones	++	13	5	++
villages	+++	29	15	++
dense human settlements with few green zones/trees	+++	26	37	+
city centres and similar habitats lacking green zones/trees	+++	16	21	–
alpine habitat	+++	5	0	–

Table 2. Variation of six plumage features based on images of 76 male Black Redstart x Common Redstart hybrids (plus 14 images of returning males from subsequent years, since adults can differ from 2CY birds). Note that not all features could be assigned for all birds. BR = *gibraltariensis*, CR = *phoenicurus*. Note that types 1–3 are merged in one column, since they differ only in the presence/absence of the white wing-panel and the (size of the) white forehead patch.

feature		types 1–3 (‘classic’)	type 4 (‘pale’)	type 5 (similar to <i>phoenicurus</i>)	type 6 (hybrid or red-bellied <i>gibraltariensis</i>)	total (n)	total (%)
white wing-panel	absent	14	9	6	0	29	38
	hint, whitish margins on (some) secondaries	11	0	1	0	12	16
	present, but clearly less than in BR, white prominent, solid	18	0	0	0	18	23
	white as BR	8	0	0	10	18	23
forehead	white forehead as CR (prominent, solid white, widest over bill)	12	2	6	0	20	25
	some white feathers, not solid patch	38	6	2	1	47	59
	no white feathers	3	1	0	9	13	16
black bib	black bib as CR	1	0	1	0	2	2
	black bib larger than CR, but similar shape, red triangle	27	7	7	0	41	51
	black bib clearly more extensive than CR, sides black	17	2	0	0	19	23
	breast black, horizontal line	9	0	0	6	15	18
	red up to belly	1	0	0	4	5	6
black/red transition	sharp, clear line	2	3	3	0	8	10
	sharp, but irregular line	33	3	4	0	40	49
	indistinct (few feathers ‘mixed’)	15	3	1	3	22	27
	poorly defined transition	4	0	0	7	11	14
belly patch	as CR	11	5	3	1	20	31
	prominent, but less than CR	16	0	1	4	21	33
	only between legs	19	0	2	2	23	36
	absent	0	0	0	0	0	0
back	grey as CR	5	4	1	0	10	14
	dark grey (darker than CR)	25	2	3	1	31	45
	greyish-black	16	0	2	8	26	37
	black	2	0	0	1	3	4

Plumage variation

All photographed male hybrids were assigned to one of six hybrid phenotypes (table 2). Three of these (types 1, 2 and 3) largely correspond to birds illustrated in Nicolai *et al.* (1996). In such birds, the black bib is clearly larger than in *phoenicurus*, but it is still restricted to the breast and it has neat edges. Types 1, 2 & 3 – defined here as ‘classic types’ – differ in the presence or absence of a white wing-panel and the amount of white on the forehead (see fig. 5); 69% of hybrids were assigned to these three phenotypes. The remaining types are 4 (birds with an extremely pale, cream to greyish body with only slight orange hue; 10%), 5 (birds that are very similar to *phoenicurus*, but for which the size of the black bib clearly exceeds the normal variation; 12%), and 6 (males with a rusty-orange belly and (lower) breast, which are otherwise extremely similar to *gibraltariensis* – i.e. hybrid or red-bellied *gibraltariensis*; 9%). Birds of all six phenotypes show some variation in plumage features

usually considered important in redstart hybrids (Steijn 2005; van der Spek & Martinez 2018).

Some of the observed variation is age-related. The ‘pale’ type 4 seems to be a first-summer phenotype: all ‘pale’ birds showed signs of immaturity, such as worn brown primaries. Moreover, there were two records from Germany where a hybrid with orange underparts was observed at exactly the same location where a territorial pale bird was present a year earlier. Other variation seems to be related again to age, but also to wear. As in *gibraltariensis*, a prominent white wing-panel appears only in adult males (14 of 22 birds aged as 3CY males or older showed a large panel); 84% of all March and April hybrids (both aged and non-aged birds) showed a white wing-panel. The panel seems to be (partly) lost through wear as the spring progresses, however: only 20% of the birds photographed in May and June showed a pale panel although there is no reason to assume that there should be fewer adults among them. In

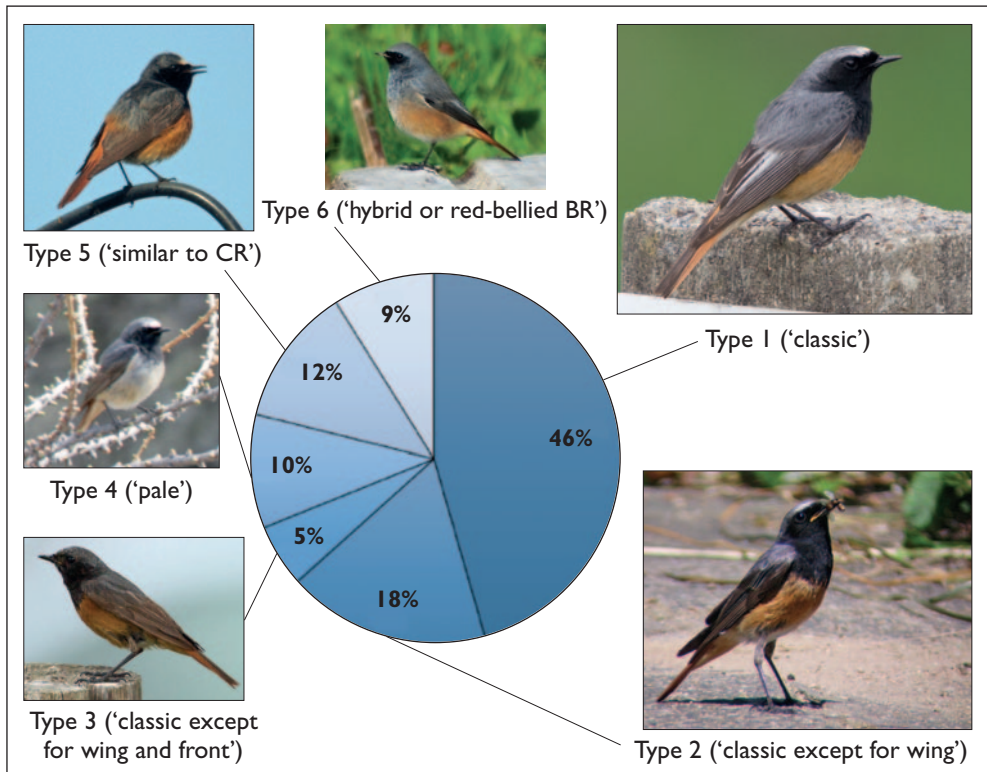


Fig. 5. Proportion of male Black Redstart x Common Redstart hybrids (n=76, plus 14 images of returning males) assigned to six hybrid phenotypes.

Image credits (clockwise from Type 1): M. Frede, T. Sørensen, H. Blockx, A. Barras, J. Honold, M. Roost.



V. Keinath

112. Photographs of the same adult (3CY+) Black Redstart x Common Redstart hybrid, Hausen, Germany, 2007. These images, taken in April, May and July (left to right), illustrate how the white wing-panel is lost due to wear. This individual is separable from Eastern Black Redstart by (for example) the large wing-panel and large forehead patch, though the quality of these images does not allow all relevant features to be checked.

addition, several known adult birds in May and June lacked a white wing-panel (plates 112 & 113). A feature that changes after the post-breeding moult is the transition between the black bib and the orange belly: new greyish feather margins result in a somewhat indistinct edge between the black bib and the orange belly in autumn. Consequently, the black bib often appears larger in autumn hybrids. Similarly, the white forehead seems to be obscured by greyish feather margins after moult in autumn (plate 114).



N. Martinez

113. Adult (3CY+) male Black Redstart x Common Redstart hybrid with heavily abraded wing feathers, Wenslingen, Switzerland, 1st July 2017. Because of the heavy wear, the white wing-panel, which may previously have been quite obvious, is barely visible.

Phenotypes of captive-bred birds

Since the origin of captive-bred birds is certain, we also studied the seven birds at Museum Heineanum (fig. 6) and additional pictures of captive-bred hybrids from Radolfzell (plate 115). Our analysis led to the following conclusions:

1. All captive male F1 hybrids belong to one of the three 'classic' types (table 2).
2. First- and second-calendar-year males lack the white wing-panel. As in *gibraltariensis*, the white feather margins are present only



L. Fitze

114. Typical autumn male Black Redstart x Common Redstart hybrid, Teufen, Switzerland, 27th August 2017. This bird shows a solid white wing-panel and greyish fringes to the breast feathers, which produce a diffuse border between dark breast and orange belly. The primary spacing in the closed wing (the ratio of P6–P7: P5–P6 equals 1:1.1 in this bird and excludes a red-bellied *gibraltariensis*). It can be told from Eastern Black Redstart by the square grey breast-patch, lacking an orange 'triangle' on the breast sides, a large amount of white on the underparts, the large white wing-panel and large white forehead patch.

after the second complete moult of 2CY birds in autumn. The white wing-panel was present in adult male birds of both parental combinations (fig. 6). However, based on our data we cannot establish whether a white wing-panel is always present in adult male F1 hybrids, regardless of the parental combination.

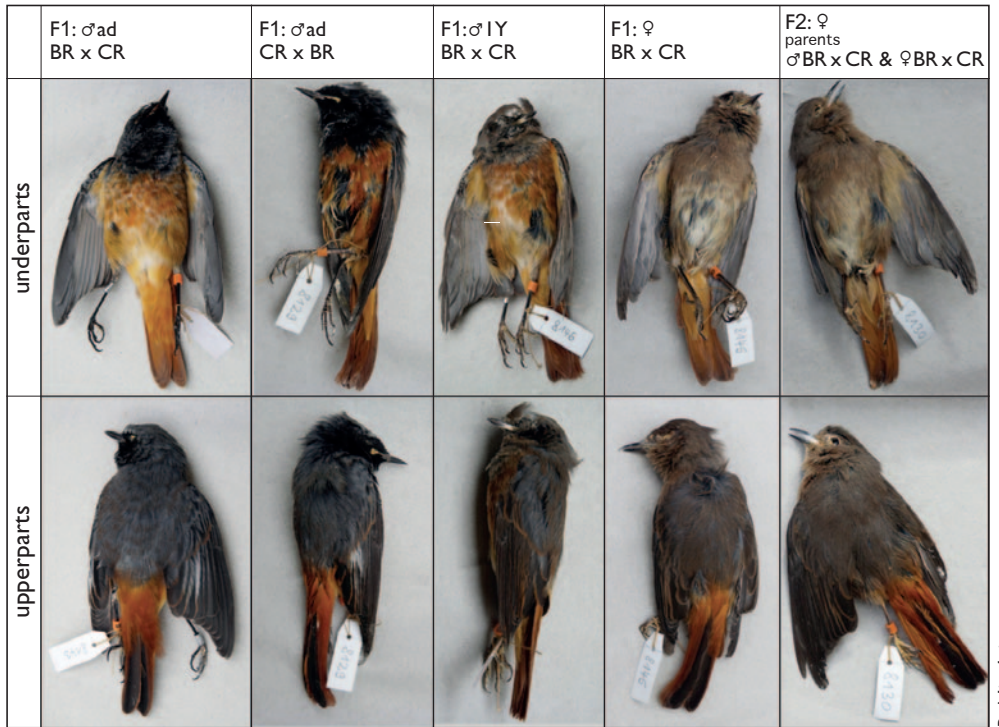
3. The extent of the black bib on the throat and upper breast is quite constant in the males analysed. Measured from bill base to centre of the breast, the bib is approximately 35 mm deep. The edge between the black bib and the orange belly was somewhat indistinct in the captive birds, owing to the presence of fresh feather margins after the post-breeding moult.
4. The white belly-patch was indistinct and did not reach further than the upper belly in both 1CY and adult males. None of the birds had the belly 'divided in two', which is commonly observed in *phoenicurus* and regularly in wild hybrids.
5. Body feathers on the back, the greater coverts and the tertials of all males had prominent rusty margins, sometimes even

giving the impression of a rusty wing-bar. These must have been inherited from *phoenicurus* and they would be buff to greyish in an Eastern Black Redstart (see Box 1).

6. Female hybrids are extremely indistinct. Although they are possibly a little warmer toned, the females examined would almost certainly be identified as *gibraltariensis* in the field. The same applies for the F2 female illustrated in fig. 6.
7. The only documented male backcross was the offspring of a hybrid female and a *gibraltariensis* male (plate 115). The edges of the black bib are less neat in this bird than in F1 hybrids and the orange on the belly is less intense.

Measurements

Most measurements of hybrids are, predictably, intermediate between those of their parental species (table 3). The only exception is the tail length of males, which seems to be more comparable with that of *gibraltariensis*. The intermediate nature of hybrids is especially obvious in terms of wing shape: in



B. Nicolai

Fig. 6. Variation in captive-bred male and female Black Redstart (BR) x Common Redstart (CR) hybrids from Vogelwarte Radolfzell.



U. Querner



V. Keinath

115 & 116. Captive-bred male backcross (male *P. o. gibraltariensis* x hybrid, autumn bird) from Vogelwarte Radolfzell, and a juvenile backcross of a pair formed by a male hybrid and a female *gibraltariensis*.

gibraltariensis the wing-tip is formed by four primaries (P3–P6, numbered ascendantly), whereas in *phoenicurus* the wing-tip is formed by three (P3–P5). The wing shape of hybrids is intermediate and the primary length of P5, P6 and P7, as well as their relative distances, enable *gibraltariensis* and *phoenicurus* to be excluded in many cases. Thus 72% of hybrids have a ‘primary spacing ratio’ (P6–P7:P5–P6) between 1:1.2 and 1:2.0, which is out of the range for both *gibraltariensis* and *phoenicurus*. Note, however, that seven out of 36 birds (19%), including five wild birds, showed ratios >1:1.5, falling in the range of *P. o. phoenicuroides* (1:1.57–2.14; Steijn 2005). As expected, backcrosses of hybrids with *gibraltariensis* approach *gibraltariensis* in morphology. Again, the number of birds examined is low and variation in length of P6 is high, with two birds showing extreme values resulting in primary spacing ratios outside the range of the parents, possibly indicating a transmission error in these two cases.

Vocalisations

According to the observers, 37/55 (67%) hybrids gave song resembling *gibraltariensis* while another 12 (22%) gave either both parents’ songs (three birds) or a mixed song (nine). Only five (9%) consistently sang like *phoenicurus*, while one bird was reported to sound similar to a singing Common Chaffinch *Fringilla coelebs*. There was no

detectable geographical difference.

At first sight, sound recordings of 14 different hybrids confirm the observers’ information: 153 strophes were strongly reminiscent of the full song of *gibraltariensis* (including a ‘scratchy’ or heavily modulated part), while 78 strophes corresponded with *gibraltariensis* partial song (without scratchy parts) and 37 strophes sounded like a mixture of *gibraltariensis* and *phoenicurus*. However, the recordings yielded no typical *phoenicurus* strophes at all.

The hybrid strophes corresponding with *gibraltariensis* seemed to be delivered at a higher pace, however, and may recall *phoenicurus* in this respect (fig. 7). The mean strophe length (full strophes) was 2.7 ± 0.4 seconds (range 1.6–4.1) and, for full strophes that include the scratchy part, the mean length of the gap between the first part and the scratchy part is 0.3 ± 0.2 seconds (range 0.0–1.4, with 86% <0.5 seconds). Corresponding values based on 65 full strophes from ten different individual *gibraltariensis* are 3.8 ± 0.5 seconds (strophe length, range 3.2–6.4), and 0.8 ± 0.6 seconds (gap before scratchy part, range 0.1–3.6, with 65% >0.5 seconds, recordings from www.xeno-canto.org). In *phoenicurus*, strophe length is 0.9–2.9 seconds (Ayé *et al.* 2014), with the upper values corresponding to complete strophes. Furthermore, some hybrids start their song with an element that may recall the introductory whistle typical of

Table 3. Mean values for basic morphological measurements of Black Redstart x Common Redstart hybrids and backcrosses compared with *phoenicurus*, *gibraltariensis* and *phoenicuroides* (measurements in mm). WL: wing length, TL: tail length, Ta: tarsus, FSp: foot span, Bb: bill depth (at feathering), Bm: bill depth (at nostrils), P: primary (feather length). Sources: Erran 2002 (WL, TL, Ta, P), Grosch 2000 (Fsp, Bb, Bm), Steijn 2005 (primary spacing ratio in *P. o. phoenicuroides*), Erran 2002 combined with data of wild hybrids (primary spacing ratio, emarginations).

		<i>phoenicurus</i>		hybrid		backcross with <i>gibraltariensis</i>		<i>gibraltariensis</i>		<i>phoenicuroides</i>	
		x ± SD	n	x ± SD	n	x ± SD	n	x ± SD	n	x ± SD	n
WL	♀	78.8 ± 2.10	7	82.6 ± 3.25	7	82.0 ± 2.65	3	84.4 ± 2.37	16	—	—
	♂	80.6 ± 2.57	65	85.3 ± 1.90	6	84.5 ± 1.80	3	86.7 ± 1.60	32	84.7 ± 2.71	27
TL	♀	54.4 ± 1.79	7	57.5 ± 1.35	7	59.0 ± 1.41	3	59.5 ± 2.14	16	—	—
	♂	56.6 ± 2.19	65	60.7 ± 2.07	6	60.8 ± 1.53	3	60.3 ± 2.10	33	60.9 ± 2.16	27
Ta	♀	21.6 ± 0.76	7	21.8 ± 0.98	7	21.7 ± 0.75	3	22.7 ± 0.94	16	—	—
	♂	22.7 ± 0.95	65	22.9 ± 0.80	6	22.4 ± 0.15	3	23.9 ± 0.75	33	24.7 ± 0.89	22
FSp	♀ & ♂	23.0 ± 0.10	19	24.0 ± 0.20	14	—	—	24.0 ± 0.10	20	—	—
Bb	♀ & ♂	3.70 ± 0.10	19	3.6 ± 0.10	14	—	—	3.40 ± 0.10	20	—	—
Bm	♀ & ♂	3.20 ± 0.00	19	3.1 ± 0.10	14	—	—	2.90 ± 0.10	20	—	—
P5	♀	61.0 ± 1.32	7	64.7 ± 1.47	7	65.3 ± 1.8	3	67.8 ± 1.47	16	—	—
	♂	64.8 ± 2.10	65	67.8 ± 1.40	7	68.7 ± 2.4	3	71.0 ± 1.39	33	—	—
P6	♀	58.0 ± 2.00	7	61.9 ± 0.94	7	63.7 ± 1.4	3	66.3 ± 1.33	16	—	—
	♂	60.1 ± 1.83	65	64.2 ± 1.08	7	64.8 ± 3.3	3	68.7 ± 2.11	33	—	—
P7	♀	54.6 ± 1.03	7	58.3 ± 1.19	7	59.5 ± 1.3	3	61.9 ± 1.32	16	—	—
	♂	57.3 ± 1.77	65	59.8 ± 1.29	7	60.2 ± 1.0	3	64.3 ± 2.95	33	—	—
Primary spacing ratio	♀ & ♂	0.90	72	1.28 ± 0.32	36	2.20 ± 1.4	6	2.29	49	2.19	10
[P6–P7:P5–P6] (range)		(0.41–1.17)		(0.88–2.25)		(0.4–4.5)		(2.00–2.50)		(1.57–3.0)	
P6 emargination [presence]	♀ & ♂	0%	72	45%	22	50%	6	100%	49	74%	27
P6 emargination length [when present] (range)	♂	—	72	11.0 ± 2.1	6	15.0 ± 0.0	2	18.4 ± 1.69	33	16.8 ± 1.47	20
				(7–13)				(14–19)			

phoenicurus, but note that *gibraltariensis* can start its strophes the same way.

A similar pattern was found in hybrid calls: the majority ($n=13$) called like *gibraltariensis*, whereas two called like *phoenicurus* and three gave both call types.

Of 43 mixed singers (the birds that looked like pure *phoenicurus* but regularly produced *gibraltariensis* song strophes), 17 consistently sang like *gibraltariensis*. Of the remainder, 12 alternated between *gibraltariensis*

and *phoenicurus* strophes, five sang strophes of both species as well as intermediate strophes, three altered between *gibraltariensis* song and intermediate strophes and six sang only intermediate strophes. We have information on calls for just nine mixed singers: three called like normal *phoenicurus*, three like *gibraltariensis* and three produced both call types.

Since only two singing birds were sound-recorded, we cannot present a general synthesis, but for these two birds, 50 strophes were analysed: 24 strophes were strongly reminiscent of *gibraltariensis* full song (11 with, 13 without the scratchy part); seven strophes corresponded to typical *phoenicurus* strophes; and 19 strophes sounded like a mixture of the two, several starting with scratchy elements (fig. 8).

As in many hybrids, the strophes corresponding to *gibraltariensis* full song were given at a faster pace and recalled *phoenicurus* in this respect: mean length of such strophes was 2.9 ± 0.6 seconds (range 2.3–3.5, with one exception that lasted 5.3 seconds); and, for strophes with the scratchy part, the mean length of the gap between the first part and

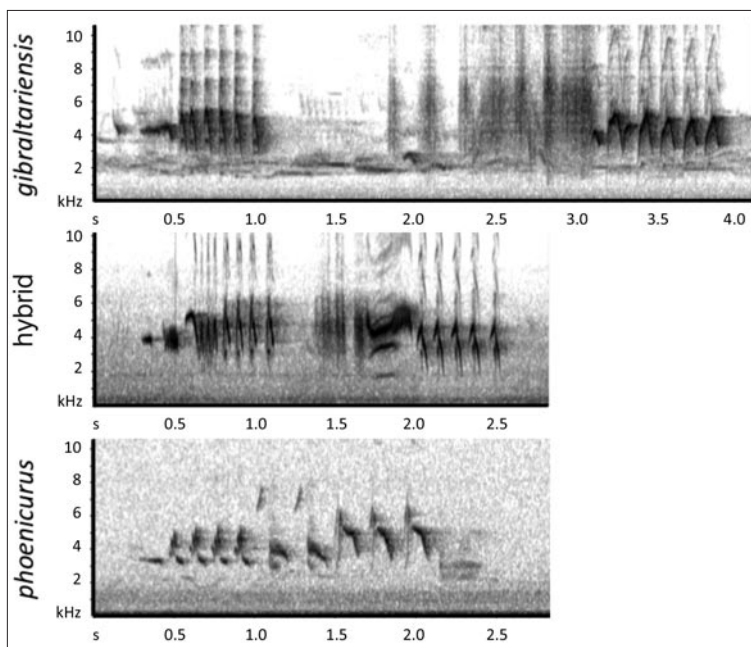


Fig. 7. Examples of a typical song strophe from a Black Redstart x Common Redstart hybrid (classic type – Venslingen, Switzerland, 2nd July 2017, based on a recording from T. Lüthi) compared with typical *gibraltariensis* and *phoenicurus* song strophes (based on recordings by NM, made in Switzerland).

the scratchy part was 0.4 ± 0.2 seconds (range 0.1–0.6).

Discussion

With 121 hybrids and 29 mixed pairs documented, redstarts are among the most frequently recorded European passerine hybrids between two clearly separated species (McCarthy 2006). Hybrids were observed throughout Europe in areas where both parental species occur; the northern limit corresponded with the northern limit of *gibraltariensis*. An exponential increase in observations over the past 30 years was noted, reflecting greater observer awareness and coverage and the easy availability of records from online databases, while the number of records from Switzerland, Germany and the Benelux countries is also likely to reflect the authors' locations. However, several other factors are probably implicated. Following the range expansion of *gibraltariensis* and the colonisation of human settlements, multiple secondary contact zones emerged (Cramp 1988; Ertan 2002; Hagemeijer & Blair 1997).

Continued on page 204

Separation of 'Eastern Black Redstart' from Common Redstart and hybrids

BOX I

Nicolai *et al.* (1996) were the first to address the identification problems of separating male 'Eastern Black Redstart' *Phoenicurus ochruros phoenicuroides* from a hybrid Black Redstart × Common Redstart. Steijn (2005) mentioned several plumage features of hybrids, but it is the wing-formula differences he described that are usually considered diagnostic. Van der Spek & Martinez (2018) tackled differences in plumage in more detail. They showed that virtually all male hybrids can be distinguished from Eastern Black Redstart by using a combination of plumage characters. They also stressed that the wing-formula differences already described by Steijn (2005) show more overlap than most birders realise; nonetheless, they remain important and may be crucial in the case of tricky individuals.

Structure (Steijn 2005; present article)

General: although likely to be a small minority, some hybrids may show a wing formula similar to Eastern Black (see table 3).

Emarginations: Eastern Black shows an emarginated P6 (numbered ascendantly, i.e. P1 is outermost) ⇨ in Common, P6 is not emarginated, while in hybrids the emargination may be missing or reduced (this is often hard to judge in photographs).

Wing-tip: in Eastern Black the wing-tip is formed by P5 (P4 & P5 equally long) ⇨ in Common, the wing-tip is formed by P4 (P3 & P4 equally long), while in hybrids it is variable (P4 or P5).

Primary spacing ratio: in Eastern Black the distance between the tips of P6 and P7 is roughly twice as long as the distance between P5 (wing-tip) and P6 ⇨ in Common, the spacing is roughly equal, while in hybrids P6–P7 is about 1.5x that of P5–P6, but in extreme cases can overlap with both Eastern Black and Common.

Plumage of male birds (from van der Spek & Martinez 2018)

- Hybrids can show a large white forehead patch, as in Common ⇨ autumn/winter Eastern Black usually has a smaller white patch or white spotting but occasionally shows more extensive white.
- Around half of all hybrids show a largely or completely grey/black area between the black



I 17. Eastern Black Redstart, ICY male, Skinninggrove, Cleveland, November 2016. Primary ratio P6/7:P5/6 equals 1:1.75 in this bird, which is typical for *phoenicuroides* but at the upper end for a hybrid. The presence of an orange triangle on the breast-sides, the lack of a white wing-panel and limited white on the forehead are plumage characters that clearly point towards an Eastern Black Redstart. *David Aitken*

breast-patch and alula/lesser/median coverts ⇒ in Eastern Black there is invariably an orange 'triangle' visible between breast-patch and wing-coverts.

- In some hybrids, the black breast-patch reaches the lower breast or even the belly ⇒ in Eastern Black the breast-patch never extends this far down the breast.
- Hybrids occasionally show a square-shaped breast-patch ⇒ in Eastern Black it is always oval.
- The edges of the breast-patch are often poorly defined in hybrids ⇒ usually fairly neat in Eastern Black.
- Hybrids can show grey or black feathers on the flanks ⇒ invariably orange in Eastern Black.
- Hybrids occasionally show isolated grey or black spots within the orange underparts (often hard to judge in poor photographs) ⇒ probably never present in Eastern Black.
- A small minority of hybrids show pale underparts, with a faint orange hue at most ⇒ the underparts are invariably vivid orange in Eastern Black.
- The undertail-coverts are whitish (sometimes with a faint orange hue) in 20% of hybrids ⇒ the undertail-coverts are orange in Eastern Black, although sometimes less vivid orange than the belly.
- Around half of all hybrids show a broad, pure white band on the belly, reaching the breast or even the breast-patch (dividing the belly in two) ⇒ fresh Eastern Black often shows narrow white fringes to orange belly feathers, but these are never broad and do not 'split' the belly.
- A small white wing-panel is commonly found in hybrids ⇒ Eastern Black may show a small wing-panel (*contra* Steijn 2005), even with whitish edges, but the vast majority show tertiaries and secondaries edged buff rather than white.
- A large white wing-panel (as in adult Western Black) is found in a quarter of hybrids ⇒ never in Eastern Black.
- In hybrids, rufous fringes to the greater-coverts and tertiaries occasionally form a small, rufous wing-bar (often hard to judge in photographs) ⇒ these fringes are buff to greyish in Eastern Black.
- Most hybrids have orange axillaries, but some show no or limited orange ⇒ the axillaries are invariably orange in Eastern Black (and in Common).

Note: van der Spek & Martinez (2018) can be downloaded from www.turnstones.org/the-eastern-black-redstart-id-pages with additional information and photographs.



118. Eastern Black Redstart, ICY male, Scalby, Yorkshire, November 2014. The dark breast-patch is restricted to the upper breast and has fairly neat edges; the area between the breast-patch and the wing-coverts is orange; narrow white fringes to the orange belly feathers are present but very restricted (no broad white band on belly); and the undertail-coverts are vividly orange.
Graham Catley

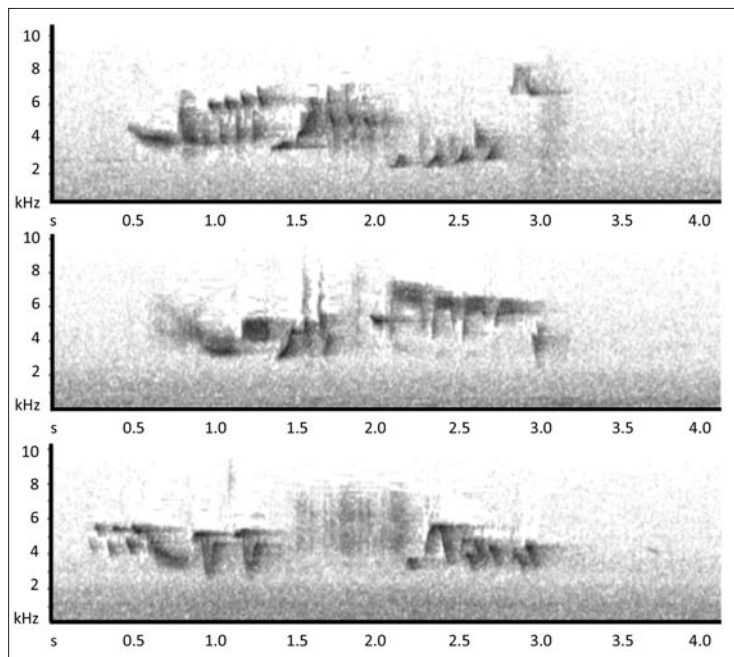


Fig. 8. Three examples of song strophes from a mixed singer (Ziefen, Switzerland, 2014, from recordings by S. Hohl and NM) showing variation from typical *phoenicurus* strophes to rather typical *gibraltariensis* strophes. Strophe length never exceeded 3.4 seconds in this bird.

Furthermore, *phoenicurus* has declined markedly in its European breeding range over the past century (Bruderer & Hirschi 1984; Zwarts *et al.* 2009). These opposing trends may mean that it is more difficult for individuals of the locally rarer species (*gibraltariensis* in Fennoscandia, *phoenicurus* in parts of central Europe) to find a mate of their own species. Köpke (1986) suggested that the increased occurrence of isolated male *phoenicurus* might have led to an increase of mixed singers and hybridisation. Note, however, that in the past 20 years or so, *phoenicurus* has apparently increased in several European countries (PECBMS 2010). We found few hybrids from eastern Europe, but assume that observations will increase following the continuing eastward spread of *gibraltariensis*. Experiments with captive birds (Berthold *et al.* 1996; Grosch 2000; Ertan 2002) demonstrated that hybrids are fertile and can have viable offspring, which showed intermediate characters (Lambert 1997; Salzmann & Soerensen 2014; plates 115 & 116). Male hybrids seem to pair mostly with a female of the locally more abundant species, as in mixed pairs. Gene flow is thus likely to flow

‘into’ *phoenicurus* in the north and *gibraltariensis* in central Europe. The (rare) incidence of *gibraltariensis* females producing bluish eggs (Nicolai 1995) may be a result of such gene flow.

The apparent lack of wild female hybrids is clearly related to the reduced detectability of birds with plumages intermediate between *gibraltariensis* and *phoenicurus*. Furthermore, the heterozygous sex (ZW; females in birds) is absent, rare, or sterile in hybrids (‘Haldane’s Rule’; Haldane 1922). Yet

breeding experiments show that fertile females occur, although we were unable to trace the sex ratio of these captive-bred birds.

The arrival dates of *phoenicurus*, *gibraltariensis* and hybrids in central Europe seem to confirm the intermediate migratory behaviour observed in experiments (Berthold & Querner 1995; Berthold *et al.* 1996). Records of hybrids on 7th March 1997 in Rome (Bulgarini & Fraticelli 1998), on 24th March 2005 in the Balearic Islands (Pérez-García & Sallent 2011), on Lampedusa on 2nd April 2007 (Brichetti & Fracasso 2008) and 12th October 2012 (G. Papale *in litt.*), and in Morocco on 27th October 2008 (Demey 2009) and 30th December 1998 (Robel & Nicolai 2009) – plus the apparent lack of hybrids during winter in central and northern Europe – suggest that hybrids winter in southernmost Europe and North Africa. This intermediate strategy has no obvious negative impact on survival, since several birds returned to the same territory in consecutive years, two being observed in four consecutive years (Nowak 1999; Lang *in litt.*).

Most hybrids are found in typical *gibraltariensis* habitats. This could indicate a

genetic preference or could be the result of birds occupying habitat similar to their hatching grounds: many migrating passerines, including redstarts (own data), later breed at or close to the site where they hatched. However, detectability is higher in habitats occupied by *gibraltariensis*, which are usually more open (hence birds are more visible) and with a higher density of human observers than those of *phoenicurus*.

The plumage variation of male hybrids is higher than previously documented and includes differences between first-summer (2CY) and adult birds and differences related to moult. It is worth re-emphasising that we do not know the genetics of wild birds. Classic-looking birds are likely to be F1 hybrids, an assumption supported by captive F1 birds. Others could be backcrosses, especially in the case of individuals strongly resembling *phoenicurus* or *gibraltariensis*. These are the most problematic phenotypes, difficult or impossible to separate from aberrant pure birds (plate 119). For instance, seemingly pure *gibraltariensis* with red bellies are known to occur. We found two examples of birds examined in the hand with rusty-orange feathers on the belly and lower breast that otherwise showed all the features of *gibraltariensis*, including wing formula (Nowak 1999;

<https://britishbirds.co.uk/birding-resources/key-refs>).

Such birds are generally thought to be aberrant or 'extreme' *gibraltariensis*, since 'normal' birds can show a variable amount of red on the lower belly and undertail-coverts (Cramp 1988). Eleven birds with limited red on the belly, and in some cases the lower breast, were considered to be red-bellied *gibraltariensis* (including the two birds men-

tioned above). However, backcrosses with a wing formula identical to *gibraltariensis* cannot be excluded without genetic analyses. Furthermore, the red belly could also be the result of a former hybridisation event that occurred several generations earlier.

We conclude that red-bellied *gibraltariensis*, reminiscent of nominate *ochruros*, are genuinely rare. Based on our own studies, the proportion lies well below 0.5%, which corresponds with data from the Swiss Ringing station at Subigerberg, where only one of 786 adult male *gibraltariensis* captured since 1980 was red-bellied (T. Roth & T. Lüthi *in litt.*). This contradicts a study mentioned in Cramp (1988), in which 8% of *gibraltariensis* showed a red belly. However, the latter was based on a sample of only 50 birds from one site in which four birds had 'belly and vent tinged rufous'. It seems likely that some of those birds had rusty tones on some belly feathers only, which is more common and does not recall typical *ochruros* (pers. obs.). Classic hybrid types, notably the forms without an obvious wing-panel, can be difficult to tell apart from Eastern Black Redstarts. Yet, through the combination of several plumage features, only a small percentage of hybrids is truly challenging (see Box 1; also van der Spek & Martinez 2018).



M. Roost

119. Redstart sp., Gurnigel, Switzerland, 21st September 2008. This bird shows a black facial mask, white wing-panel, no apparent white forehead, greyish-orange flanks and belly, and diffuse breast-patch delimitation on the upper breast; it is thus classified as a hybrid or a red-bellied *gibraltariensis* (type 6) in the present study. Without biometrics, such birds are best left unidentified. Eastern Black Redstart can be excluded by the large, square-shaped breast-patch (lacking the 'orange triangle'), and the seemingly large white belly-patch that divides the orange belly in two. The white wing-panel is also relatively large.

There are two distinct plumages in immature male *gibraltariensis*. After the post-juvenile moult, approximately 12% of ICY males develop a blackish body similar to adult males: the ‘*paradoxus* morph’ (Kleinschmidt 1907/08; Nicolai *et al.* 1996). Since they retain juvenile flight feathers, however, they lack the white wing-panel of an adult male (birds that moult some tertials will show a very narrow ‘panel’, formed by the tertial edges). The majority of ICY males, the ‘*carei* morph’, are essentially female-like. As far as we know, there are no observations of either wild or captive hybrids of the ‘*carei* morph’. Conceivably, the pale hybrid type is related to this morph, but we conclude that the ‘*carei* morph’ is much rarer – if not absent – among hybrids.

Our findings confirm that the primary spacing ratio and an emarginated P6 are good features for identification of F1 hybrids. However, there is substantial overlap with both parental species, and even more so with Eastern Black Redstart of the race *P. o. phoenicuroides* (see table 3 and Box 1 for more information). Furthermore, backcrosses occur in the wild and measurements of captive backcrosses show that they can approach either species.

In a significant proportion of the mixed pairs, *phoenicurus* males were mixed singers. For obvious reasons, their song may be more attractive to *gibraltariensis* females and their habitat choice probably facilitates mixed pairings, too. At first glance, *gibraltariensis* seems to be dominant in song and call and therefore many hybrids will probably go unnoticed when heard only. This is mainly due to the scratchy part: if present, this would normally lead an observer to identify the song as that of *gibraltariensis*, even if other aspects – for example pace and strophe length – are not typical. McCarthy (2006) suggested that the similarity of hybrid and *gibraltariensis* song may be due to the fact that *gibraltariensis* usually plays the role of male parent in this cross. He probably overestimated the similarity, however, and his explanation ignores the fact that *phoenicurus* is the male parent in most mixed pairs in central Europe. Nonetheless, many mixed broods occur in habitats more typical for *gibraltariensis* and the song of adjacent males

may have been dominant there. We did not, however, see any geographical patterns in terms of song, with *gibraltariensis* song being the dominant song for both mainland European and Fennoscandian hybrids.

Songs of mixed singers by definition contain *gibraltariensis* elements, but are otherwise highly variable. Pace and song length is generally typical for *phoenicurus*, however, even in strophes that strongly recall *gibraltariensis*, which largely corresponds with previous studies (Hegelbach & Nabulon 1998; Brehme & Michaelis 2017). Without genetic data, we can only speculate about the identity of mixed singers. They could be normal *phoenicurus* that imitate *gibraltariensis*, probably because they copied elements of *gibraltariensis* song after they fledged. Several mixed singers also gave *gibraltariensis*-like calls, however, and since it is sometimes assumed that calls have a stronger genetic component than song, this could point towards a hybrid origin.

Since male hybrids normally breed with *gibraltariensis* females in central Europe, it would be expected that, unlike mixed singers, backcrosses should approach *gibraltariensis* in plumage, although lack of knowledge of female hybrids is a gap in our understanding here. In terms of mixed singers, we conclude that if they are genetically pure *phoenicurus*, imitation of song is an important factor for hybridisation between the two species, since song differences are likely to form the strongest prezygotic isolation barrier (Grosch 2000). However, if mixed singers are backcrosses, they are simply a direct consequence of a former hybridisation event. Genetic analyses would be extremely helpful to answer this open question.

Landmann (1987), Berthold *et al.* (1996) and Ertan (2002) have already suggested the existence of gene flow between *gibraltariensis* and *phoenicurus* through introgressive hybridisation. Grosch (2003) suggested that gene flow between both species might be limited by prezygotic rather than postzygotic isolation, and that differences in habitat choice as well as song may form the strongest isolation barriers. Separation through habitat factors is reduced in secondary contact zones near human settlements, and gene flow between the species in Europe may therefore

continue to increase. In the long term, this could even influence speciation, since new genetic variance introduced by hybridisation is estimated to be 2–3 times higher than in gene mutation (Grant & Grant 1994).

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Appendix 1.

Records of hybrids between Black Redstart *Phoenicurus ochruros* and Common Redstart *P. phoenicurus*, red-bellied *P. o. gibraltariensis* and hybrid claims considered in the article. Categories: 1 = confirmed hybrid (wing measurements); 2 = confirmed hybrid (images); 3 = confirmed hybrid (description and/or earlier publication); 4 = unconfirmed hybrid (claims without description or images; also records of 'Eastern Black Redstart' *P. o. phoenicuroides* not accepted by national rarity committees when a hybrid was considered the more likely option); 5 = hybrid or 'red-bellied' *gibraltariensis*; 6 = 'red-bellied' *gibraltariensis*.

Details of each record (separated by /) are presented in the following sequence: date (day.month.year), location, country, reference and category. Country codes: AL – Albania, AT – Austria, BE – Belgium, CH – Switzerland, DE – Germany, DK – Denmark, ES – Spain, FI – Finland, FR – France, GB – Great Britain, IT – Italy, LU – Luxembourg, MA – Morocco, NL – the Netherlands, NO – Norway, PL – Poland, SE – Sweden, UA – Ukraine.

1889, Marburg, DE (Kleinschmidt 1903) cat. 6 / 18.04.1906, Taucha bei Leipzig, DE (Kleinschmidt 1907/08) cat. 3 / May 1929, Meurthe-et-Moselle, FR (Heim de Balsac 1929, *Bull. Muséum national d'Histoire naturelle* 2e Serie 1: 304–306) cat. 3 / 15.09.1932, Ungiasca de Cossogno, IT (Moltoni 1946, *Rivista italiana di Ornitologia*, 2nd Ser., 16: 169–172) cat. 1 / 1932, Leipzig, DE (Dathe 1950, *Ornithol. Mitt.* 2: 59–62) cat. 3 / 25.05.1948, Helgoland, DE (Ringleben 1958,

Vogelwarte 15: 40–41) cat. 3 / 13.10.1975, Bryher, Scilly, GB (Stoddart 2016) cat. 4 / 15.10.1978, Saltfleetby, Lincolnshire, GB (Stoddart 2016) cat. 3 / 1978–79, Regensburg, DE (Klose 1986, *Anz. der Ornithol. Gesellschaft in Bayern* 24: 184) cat. 3 / 03.10.1979, Flamborough Head, Yorkshire, GB (Stoddart 2016) cat. 4 / 31.05.1987, Oerlinger Ried, CH (S. Gysel in Droz 2011) cat. 3 / June 1987, Gothenburg, SE (Andersson 1988, *Vår Fågelvärld* 47: 149–150) cat. 3 / May 1988, Köln, DE (Grosch 2000) cat. 3 / 16.10.1988, Donna Nook, Lincolnshire, GB (Stoddart 2016) cat. 4 / 21.07.1989, Lac de Bouverans, FR (D. Michelat & M. Montadert in Droz 2011) cat. 3 / 02.06.1990, Harlingen, NL (A. van den Berg, <http://macaulaylibrary.org/audio/71158>) cat. 3 / 12.10.1991, Flamborough Head, Yorkshire, GB (Stoddart 2016) cat. 4 / 1992, Donzdorf-Unterweckerstell, DE (Nowak 1999) cat. 3 / 26.05.1993, Läufeufingen, CH (Blattner & Kestenholz 1993, *Ornithol. Beob.* 90: 241–245) cat. 1 / 08.10.1993, Subigerberg, CH (T. Lüthi, T. Schwaller, <https://bebbibabbler.jimdo.com>), cat. 2 / 16.05.1994, Donzdorf-Unterweckerstell, DE (Nowak 1999) cat. 4 / 29.05.1994, Oberhof, DE (Nowak 1999) cat. 3 / 15.09.1994, Donzdorf, DE (Nowak 1999) cat. 3 / 1994, Malmö, SE (Olsson 1994 in Petersson *et al.* 2014) cat. 3 / May 1995, Agadir, MA (Robel & Nicolai 2009) cat. 4 / May 1995, Casablanca, MA (Robel & Nicolai 2009) cat. 4 / 12.06.1995, Bad Harzburg, DE (Heuer 1999, *Milvus* 18: 57–58) cat. 1 / 20.04.1996, Mardorf, DE (Frauendorf, Gunther, Schrack & Ernst 1997, *Mitt. Ver Säch. Orn.* 8: 105–109) cat. 3 / 21.04.1996, Niederstetten, DE (Dornberger, Dehner & Nicolai 1996, *Faun. & Flor. Mitt. Taubergrund* 14: 36–46) cat. 1 / 22.04.1996, Insbeck Wevelinghoven, DE (Frede 2012, *Charadrius* 48: 84–86) cat. 2 / 29.04.1996, Koziencien, PL (Rebis 1998, *Not. Ornithol.* 38: 50) cat. 1 / 04.05.1996, Istein, DE (T. Stalling in Grosch 2000) cat. 2 / 12.05.1996, April 1997, Mariembourg, BE (Lambert 1997) cat. 2 / June 1996, Dessau, DE (Grosch 2000) cat. 3 / 07.03.1997, Rome, IT (Bulgarini & Fraticelli 1998) cat. 3 / 1997–2000, Schlatt, DE (Nowak 1999, *Naturkdl. Mitt. Lks. Göppingen* 18: 9–15) cat. 6 / 25.04.1998, Desues, FR (M. Giroud in Droz 2011) cat. 3 / July 1998, Hemmental, CH (H-P. Bieri, M. Roost) cat. 2 / 30.12.1998, Agadir, MA (Robel & Nicolai 2009) cat. 3 / 02.05.2000, Jyväskylä, FI (Lindholm 2001) cat. 3 / 2000–02, Ruhstein, DE (Förschler 2005, *Vogelwarte* 43: 195–198) cat. 2 / 06.06.2000, Monte Meta, IT (L. Juillerat in Droz 2011) cat. 3 / 03.10.2000, Fano, DK (Steijn 2005) cat. 1 / 23.04.2001, Porvoo, FI (Lindholm 2001) cat. 1 / 2001, Tampere, FI (Lindholm 2001) cat. 2 / 28.04.2002, Erstavik, SE (Steijn 2005) cat. 1 / 05.05.2002, Lüttau, CH (W. Burri, www.ornitho.ch) cat. 3 / 23.03.2003, Sursee, CH (S. Birrer in Droz 2011) cat. 2 / 26.05.2003, Steibach, DE (Zedler 2004, *Falke* 51: 324–325) cat. 2 / 17.03.2004, Dresden, DE (Töpfer 2005, *Mitt. Ver Säch. Orn.* 9: 74–75) cat. 3 / 13.04.2004, Groote Peel, NL (van Dongen, Haas & de Rouw 2004, *Dutch Birding* 26: 272–281) cat. 2 / 2004 Subigerberg, CH (T. Schwaller, <https://bebbibabbler.jimdo.com>) cat. 6 / 29.01.2005, Firenze, IT (D. Occhiato, www.pbase.com) cat. 6 / 24.03.2005, Cabrera NP, Balears, ES (Perez-Garcia & Sallent 2011) cat. 1 / 01.04.2005, 30.04.06, 18.05.07, Chamoson, CH (L. Maumary in Droz 2001) cat. 2 / 22.04.2005, Ospeldijk, NL (Steijn 2005) cat. 1 / 30.04.2005, 19.04.06, 08.04.07, Hausen, im Killertal, DE (B. Nicolai, V. Keinath *in litt.*) cat. 2 / 06.10.2005, Pisa, IT (D. Occhiato, www.pbase.com) cat. 2 / 27.11.2005, ES (J. M. Puig, www.geocities.ws/ocellososona_id/Phoenicurus.html) cat. 6 / 2005, 23.03.06, Saint-Laurent-de-la-Prée, FR (J. Gonin, N. Gendre, www.surfbirds.com) cat. 1 / 21.05.2006, Elstal, DE (Dürr 2007, *Oris* 15: 33–36) cat. 1 / 31.05.2006, Schöffengrund-Niederquembach, DE (Lay 2017, *Vogelkund. Hefte Edertal* 43: 63–68) cat. 3 / 13.06.2006, Grembergen, BE (Driessens 2006, *Dutch Birding* 28: 255–264) cat. 2 / 12.09.2006, Col de Jaman, CH (Droz 2011) cat. 1 / February 2007, Cadiz, ES (Tag, www.birdforum.net) cat. 5 / 02.04.2007, Lampedusa, IT (A. Corso, www.ebntalia.it) cat. 1 / 09.04.2007, Rüeggisberg, CH (www.ornitho.ch) cat. 4 / 27.04.2007, BE (G. Vermeersch, www.pbase.com) cat. 2 / 01.05.2007, Romrod, DE (Stübing, Heckmann & Roland 2013, *Vogel & Umwelt* 20: 15–78) cat. 3 / 27.05.2007, Dillenburg-Erbach, DE (Stübing, Heckmann & Roland 2013, *Vogel & Umwelt* 20: 15–78) cat. 3 / 04.04.2008, Leusden, NL (T. van de Kamp, <http://www.waarneming.nl>) cat. 2 / 10.04.2008, Villeneuve-lès-Maguelone, FR (P-A. Crochet, <http://chr.lrf.free.fr>) cat. 2 / 24.04.2008, Hindelbank, CH (www.ornitho.ch) cat. 4 / April 2008, Gothenburg, SE (Petersson *et al.* 2014) cat. 1 / 03.05.2008, Tuniberg, DE (J. Wiegand in Droz 2011) cat. 3 / 17.09.2008, Gurnigel, CH (W. & P. Oberhänsli, M. Roost, www.ornitho.ch) cat. 5 / 08.10.2008, Cap Ferret, FR (L. Barbaro, www.faune-aquitaine.org) cat. 3 / 27.10.2008, Aguelmouss, MA (Demey 2009) cat. 2 / 05.04.2009, 2010, Dobro, ES (M. Alsonso, <http://avesnortedeburgos.blogspot.ch>) cat. 2 / April 2009, LU (www.ornitho.lu) cat. 4 / 16.06.2009, 2010, Träullit, Österbyom, SE (M. Thorin, www.hoglandsobsar.se, Petersson *et al.* 2014) cat. 1 / 2009–10, Dachslern, CH (R. Wiedmer, F. Ducry, www.chclub300.ch) cat. 2 / 12.02.2010, Lincoln Cathedral, Lincolnshire, GB (M. Garner) cat. 6 / 31.03.2010, Landsende Romo, DK (I. Jensen, www.netfugl.dk) cat. 2 / 14.04.2010, Leusden, NL (R. Wilschut, <http://kansloosvogelen.blogspot.nl>) cat. 2 / 27.07.2010, Fusio, CH (S. Mombelli, www.ornitho.ch) cat. 2 / 2010–2013, Grobau, DE (Lang *in prep.*) cat. 2 / 19.03.2011, Spurn, Yorkshire, GB (M. Garner) cat. 6 / 06.04.2011, Groote Peel, NL (M. van der Velde, <https://www.waarneming.nl>) cat. 2 / 25.04.2011, Neustadt am Rübenberge, DE (Lehmhus & Rinas 2018, *Aves Braunschweig* 9: 19–30) cat. 2 / 01.05.2011, Hov, NO (<http://artsobservasjoner.no>) cat. 4 / 08.05.2011, 14.04.2012, Brockenplateau, DE (Hellmann 2015, *Ornithol. Jber. Mus. Heineanum* 33: 1–96) cat. 2 / 24.05.2011, Rodersdorf, CH (A. Capol, www.ornitho.ch) cat. 2 / 2011–12, Falun, SE (P. Adenäs in Petersson *et al.* 2014) cat. 3 / 31.03.2012, Wyhlen, DE (D. Kratzer, www.ornitho.de) cat. 2 / 03.04.2012, Burghalde u. Herrenwäldle, DE (J. Gommel, www.ornitho.de) cat. 3 / 15.04.2012, Schweina, DE (D. Volkmar, www.ornitho.de) cat. 3 / 27.04.2012, Hilchenbach, DE (Frede 2012, *Charadrius* 48: 84–86) cat. 1 / 30.04.2012, Västra Tunhem, SE (G. Darefelt, <https://artportalen.se/image/1163510>) cat. 2 / 10.05.2012, Lindberg Rindeloch, DE (T. Sacher, www.ornitho.de) cat. 2 / 13.05.2012, Ijmuiden, NL (H. de Nobel, <http://www.waarneming.nl>) cat. 2 / 28.05.2012, Picon, FR (S. Tillo, www.faune-aquitaine.org) cat. 2 / May 2012, Joensuu, FI (Normaja 2013, *Limnol* 48(2): 52) cat. 2 / 11.06.2012, Freising, DE (www.ornitho.de) cat. 4 / 29.09.2012, 20.09.13, Schollene, DE (M. Schönenberger, www.ornitho.de) cat. 3 / 05.10.2012, Rosswasen, DE (www.ornitho.de) cat. 4 / 12.10.2012, Lampedusa, IT (G. Papale *in litt.*) cat. 1 / 19.10.2012, Diekholzen, DE (H. Verdaat, www.observation.org) cat. 5 / 2012, Limhamn, SE (S. Cherrug in Petersson *et al.* 2014) cat. 3 / 27.03.2013, Gingen, DE (M. Nowak *in litt.*) cat. 5 / 22.04.2013, 29.04.14, 15.04.15, Wenslingen, CH (H. Hersberger, N. Martinez, <https://bebbibabbler.jimdo.com>) cat. 1 / April 2013, Bodensee, DE (www.ornitho.de) cat. 5 / 24.05.2013, Næroset, NO (Simon Rixx, <http://oslobirder.blogspot.ch>) cat. 1 / 03.07.2013, 09.04.2014, Wehrheim, DE (Salzmann & Soerensen 2014, *Vögel* 01/14: 82–83, <http://flickriver.com>) cat. 2 / 07.07.2013, Tiefentaler Köpfe, DE

(www.ornitho.de) cat. 4 / 13.07.2013, Eifel, DE (H. Dolmans, <https://observation.org>) cat. 2 / 13.10.2013, Skærbæk, DK (M. Elley, www.neflugl.dk) cat. 6 / 2013–14, Lllupia, FR (J. Piette, www.faune-lr.org) cat. 2 / 2013, Dortmund, DE (Frede 2012, *Charadrius* 48: 84–86) cat. 3 / 20.03.2014, Heeslingen, DE (H. Postels, www.ornitho.de) cat. 4 / 27.03.2014, Görliitz-Nikilavorstadt, DE (www.ornitho.de) cat. 4 / 22.04.2014, Mantena Hamar, NO (L. Kapelrud, www.artsobservasjoner.no) cat. 2 / 27.04.2014, Meerle, BE (<http://waarnemingen.be>) cat. 4 / April 2014, Dnipro, UA (Fesenko & Shybanov 2016) cat. 2 / 2014–2016, Fulda, DE (P. Hess, www.hgon.de) cat. 2 / 07.05.2014, Dortmund, DE (www.ornitho.de) cat. 4 / 13.05.2014, Heinsberg, DE (G. de Hoog, <https://observation.org>) cat. 3 / 13.05.2014, Usikapunki, FI (P. Alho, www.tarsiger.com) cat. 1 / 18.05.2014, Ruhenstein, DE (M. Förschler, www.ornitho.de) cat. 3 / 20.05.2014, Braunau, AT (M. Mitterbacher, www.ornitho.at) cat. 3 / 01.09.2014, Arcen en Velden, NL (H. Crommentuyn, <http://waarneming.nl>) cat. 2 / 04.01.2015, Brunsbüttel, DE (K. Dallmann, www.ornitho.de) cat. 5 / 13.01.2015, Málaga, ES (A. Paterson, <http://birdspain.blogspot.ch>) cat. 5 / 09.04.2015, les Fénis, CH (M. Muller, www.ornitho.ch) cat. 2 / 11.04.2015, Helgoland, DE (J. Dierschke, <https://birdingfrontiers.wordpress.com>) cat. 6 / 18.04.2015, Bad Laer, DE (www.ornitho.de) cat. 4 / 18.04.2015, Lammersdorf, DE (M. Lay, www.ornitho.lu) cat. 2 / 09.05.2015, Ayent, CH (A. Barras, www.ornitho.ch) cat. 2 / 13.05.2015, Hansdorf, DE (www.ornitho.de) cat. 4 / 23.05.2015, Ballern Merzig, DE (www.ornitho.lu) cat. 4 / 30.05.2015, Sylt, DE (M. Schereitz, www.ornitho.lu) cat. 2 / 04.06.2015, Hambuchen, DE (Hinterkeuser & Schmied 2015, *Berichtsheft der Arbeitsgem. Bergischer Ornithol.* 65: 30–33) cat. 2 / 08.06.2015, Hohentauern, AT (www.ornitho.at) cat. 4 / 17.06.2015, Jokioinen, FI (P. Mäkelä, www.tarsiger.com) cat. 1 / 21.06.2015, Gent, BE (H. Blockx, <http://waarnemingen.be>) cat. 1 / 18.07.2015, Vorderweidenthal, DE (N. Roth, R. Klein, www.ornitho.de) cat. 1 / 24.08.2015, Fromelennes, FR (<https://observation.org>) cat. 4 / 11.09.2015, Katzenstein, DE (E. Bezzel, www.ornitho.de) cat. 3 / 09.04.2016, Neubrandenburg, DE (www.ornitho.de) cat. 4 / 22.04.2016, Wrocław, PL (Z. Marciniak, www.facebook.com/BirdingPoland) cat. 2 / 04.05.2016, Hohenkreuz, DE (J. Mayer, www.ornitho.de) cat. 3 / 07.05.2016, Teich Junkershammer, DE (www.ornitho.de) cat. 4 / 18.05.2016, Wildschönau, AT (www.ornitho.at) cat. 4 / 26.05.2016, Vermosh, AL (Ernst 2017, *Ornithol. Jber. Mus. Heineanum* 34) cat. 1 / 03.07.2016, 09.04.2017, Rosenthal, DE (M. Lay, www.ornitho.lu) cat. 1 / 22.07.2016, Langwies, CH (P. Knaus, www.ornitho.ch) cat. 3 / 21.09.2016, Schlangenberg, DE (www.ornitho.de) cat. 4 / 03.10.2016, Haute Savoie, FR (A. Chappuis, www.ornitho.ch) cat. 6 / 08.10.2016, Vacquerie-et-Saint-Martin-de-Castries, FR (P. Gitenet, www.faune-lr.org) cat. 5 / 06.04.2017, Friedberg, DE (www.ornitho.de) cat. 4 / 13.04.2017, Bordenau, DE (Lehmhus & Rinas 2018, *Aves Braunschweig* 9: 19–30) cat. 1 / 19.04.2017, Aigen im Ennstal, AT (www.ornitho.at) cat. 4 / 28.04.2017, Gmina Lwówek, PL (Paweł Szymański, www.xeno-canto.org/366713) cat. 1 / 19.05.2017, Teufen, CH (K. Frueh, L. Fitze, www.ebird.org, www.ornitho.ch) cat. 1 / 30.05.2017, Wenslingen, CH (H. Hersberger, N. Martinez, T. Lüthi, <https://bebbibabblers.jimdo.com>) cat. 1 / 31.05.2017, Köpfingen, DE (J. Honold, www.ornitho.de) cat. 1 / June 2017, Cracow, PL (T. Stawarczyk *in litt.*) cat. 2 / 20.09.2017, Niederheim Tongeren, BE (C. Richerzhagen, E. Colson, <http://trekellen.org>) cat. 1 / 01.11.2017, San Leonardo in Passiria, IT (H. Maier, www.ornitho.it) cat. 6 / 16.11.2017, Parc Natural del Garraf, ES (N. Teufenbacher *in litt.*) cat. 5.

Appendix 2.

Records of mixed pairings between Black Redstart *Phoenicurus ochruros* and Common Redstart *P. phoenicurus* considered in the article.

Details of each record (separated by /) are presented in the following sequence: year, location, country and reference. Country codes: AT – Austria, CH – Switzerland, DE – Germany, FI – Finland, FR – France, NO – Norway, SE – Sweden.

c. 1929, FR (Heim de Balsac 1929, *Bull. Muséum national d'Histoire naturelle* (Paris) 1: 304–306) / 1959, Sköde, SE (Andersson 1963, *Vår Fågelvärld* 22: 290–291) / 1959–1960, Tirol, AT (Landmann 1987, *Ökol. Der Vögel* 9: 97–106) / 1960, Sköde, SE (Andersson 1963, *Vår Fågelvärld* 22: 290–291) / 1963, Aschersleben, DE (Böhm & Strohkorb 1964, *Beitr. Vögelk.* 10: 235–236) / c. 1963, SE (Andersson 1963, *Vår Fågelvärld* 22: 290–291) / 1980, Amiens, FR (Robert & Toulon 1984, *Aves* 21: 105–108) / 1985, SE (Orhult 1986, *Natur pa Dal* 12: 6–7) / 1985, Halberstadt, DE (B. Nicolai) / c. 1987, DE (Gaumnitz in Landmann 1987) / 1989, Muotas Muragl, CH (Ruppen & Ruppen 1990, *Ornithol. Beob.* 87: 59) / 1994, Rüdlingen, CH (Hegelbach & Nabulon 1998, *Ornithol. Beob.* 95: 129–136) / 1995, Boos an der Nahe, DE (Buchmann 2007, *Fauna und Flora in Rheinland-Pfalz*, Band 11, Heft 1) 1998–1999, Nettetel, DE (Thomas 1999, *Ornithologischer Jahresbericht für den Kreis Viersen. Nettetel.*) / 1999, Schlat, DE (Nowak 2001, *Naturkd. Mitt. Lks. Göppingen* 20: 18) / 1999, Oensingen, CH (Grosch 2000) / 1999, Freiberg, DE (Grosch 2000) / 1999, Karlsruhe, DE (Grosch 2000) / 2000, Schlat, DE (Nowak 2001, *Naturkd. Mitt. Lks. Göppingen* 20: 18) / 2005, Schlat, DE (M. Nowak *in litt.*) / 2007, Tampere, FI (J. Lindfors, www.tarsiger.com) / 2007, Turku, FI (T. Lindroos, <https://tomlindroos.lg.fi> & www.tarsiger.com) / 2008, Dornach, CH (O. Hurt, www.ornitho.ch) / 2008, Chavannes, CH (C. Plummer in Droz 2011) / 2011, Therwil, CH (N. Martinez, [www.bebbibabblers.jimdo.com](https://bebbibabblers.jimdo.com)) / 2011, Oslo, NO (<http://infoa.no>) / 2013, Hamburg, DE (Team Sammelbericht NWR 2014, *Charadrius* 50: 127–216) / 2014, Maclas, FR (<http://naturellementnature.free.fr>) / 2015, Ziefen, CH (A. Fasolin, S. Hohl, N. Martinez, Y. Wennberg, [www.bebbibabblers.jimdo.com](https://bebbibabblers.jimdo.com)).