Identification and taxonomy of northern and eastern yellow wagtails – new pieces to the puzzle

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The taxonomy of yellow wagtails *Motacilla flava* sensu lato is notorious, as evident in the extensive literature on the validity and relationships of the numerous (sub)species (see Alström & Mild 2003 for a review). Following the recent split into two species – Western Yellow Wagtail *M flava* sensu stricto and Eastern Yellow Wagtail *M tschutschensis* – by several authorities (eg, del Hoyo & Collar 2016, Gill et al 2021), interest in the complex has increased among birders. In the last decade, birds showing features associated with Eastern Yellow have been regularly recorded in Europe, although firm identification is challenging because of uncertainty regarding variation and overlap between populations.

The purpose of this paper is to present data on variation in morphometrics, plumage and vocalisations in northern and eastern yellow wagtails, and to discuss possible taxonomical implications from the results. For practical reasons, the nomenclature follows del Hoyo & Collar (2016) ('HBW'), ie, not the taxonomy normally applied in Dutch Birding (www.dutchavifauna.nl/wpvogelnamen). In the text and captions, 'yellow wagtail *Motacilla flava* sensu lato' is used as a general term to indicate all (sub)species belonging to this complex. In terms of taxa recognised by HBW, the main focus of the paper are the Arctic subspecies *M f thunbergi* (hereafter *thunbergi*), *M t plexa* (hereafter *plexa*) and *M t tschutschensis* (hereafter *tschutschensis*), and the more southerly *M t angarensis* (hereafter *angarensis*), *M t simillima* (hereafter *simillima*), and *M t macronyx* (hereafter *macronyx*). While acknowledging that some authorities, eg 'IOC' (Gill et al 2021), include *angarensis* and *simillima* in *tschutschensis* (following Alström & Mild 2003), the more detailed division in HBW is chosen as a point of departure in order to make references to geographic areas simpler. See table 1 for distributions of these taxa as given in HBW (Badyaev et al 2020, Tyler & Christie 2020), along with the distribution of other taxa mentioned more briefly in the text. The paper also discusses the form *zaissanensis* that breeds in the Altai mountains. While not considered a valid taxon by HBW or IOC, it is recognised by some other authors (eg, Red'kin et al 2016). A few additional yellow wagtail subspecies recognised by HBW are mentioned in the text when relevant.

Methods

Examined material

This paper is based on a review of existing literature, online field photographs and sound recordings, field studies and examination of museum specimens in the British Museum of Natural History (BMNH, Tring, England), Swedish Museum of Natural History (NRM, Stockholm, Sweden), Zoological Museum of the Zoological Institute of the Russian Academy of Sciences (ZIN, Saint Petersburg, Russia), Zoological Museum of Moscow University (ZMMU, Moscow, Russia), Finnish Museum of Natural History (ZMUH, Helsinki, Finland) and Natural History Museum of Denmark (ZMUC, Copenhagen, Denmark). In addition, photographs and, in a few cases, measurements of specimens have been obtained from the Institute of Systematics and Ecology of Animals of the Siberian Branch of the Russian Academy of Science (ISEA SB RAS, Novosibirisk, Russia), Krasnoyarsk Regional Museum of Local Lore (KKKM, Krasnoyarsk, Russia), Museum of Comparative Zoology (MCZ, Cambridge, USA), State Darwin Museum (SDM, Moscow), Staatliches Naturhistorisches Museum (SNMBG, Braunschweig, Germany), University of Washington Burke Museum (UWBM, Seattle, USA), Alexander Koenig Research Museum (ZFMK, Bonn, Germany) and Zoological Museum in Syktyvkar (Komi, Russia).

In order to assign studied birds to geographic origin with reasonable certainty, the study is limited to adults on breeding grounds in late May to August, and to birds in first-winter plumage in August to early September, with the exception of a short reflection on calls in migrating and wintering birds.

The numbers of examined specimens and live birds for each region are summarised in appendix 1.

TABLE 1 Overview of yellow wagtail *Motacilla flava* sensu lato taxa mentioned in this paper

Species according to HBW	**Subspecies recognised by HBW and mentioned in text**	**Breeding range as given in HBW (to be compared with figure 30)**
Motacilla flava (Western Yellow Wagtail)	*flava* Linnaeus, 1758	N & C Europe (S from S Scandinavia) E to Urals
	thunbergi Billberg, 1828	Scandinavia E to NW Siberia
	beema (Sykes, 1832)	From upper Volga river E to SW Siberia, S to N Kazakhstan and Altai Mountains
	leucocephala (Przevalski, 1887)	NW Mongolia, extreme NW China (N Xinjiang) and adjacent parts of former USSR
	feldegg Michahelles, 1830	SE Europe, S to Turkey, E Mediterranean, Arabian Peninsula, W Caspian, Iran and N Afghanistan
	flavissima (Blyth, 1834)	Britain and adjacent coastal Europe
	iberiae Hartert, 1921	Iberia, SW France and NW Africa
	lutea (Gmelin, 1774)	SW Russia to NW and NC Kazakhstan
Motacilla tschutschensis (Eastern Yellow Wagtail)	*tschutschensis* Gmelin, 1789	NE Siberia and extreme NW North America
	plexa (Thayer & Bangs, 1914)	N Siberia (Khatanga river E to Kolyma river)
	simillima Hartert, 1905	Kamchatka, N Kurils and Commander Island, and possibly Pribilofs and Aleutian Islands
	angarensis (Sushkin, 1925)	S Siberia and W Transbaikalia S to N Mongolia
	macronyx (Stresemann, 1920)	SE Transbaikalia E to Amurland and Ussuriland, S to NE Mongolia and NC and NE China
	taivana (Swinhoe, 1863)	SE Siberia, Amurland, Sakhalin and N Japan (N Hokkaido)
Additional form dealt with in this text (not recognised by HBW; considered by various authors either as subspecies of *M tschutschensis*, as synonymous with *angarensis* or *tschutschensis*, or as intergrade between these and *beema*)		
	zaissanensis (Poliakov, 1911)	According to present study at least Altai Mountains in north-easternmost Kazakstan and northern Xinjiang; possibly also Russian and Mongolian Altai

Studied features

This paper focuses on the following morphometric and plumage features, all of which have been recognised in earlier literature as useful for identification of the taxa involved (see Alström & Mild 2003 for a review): ***1*** length of hind claw; ***2*** distance between wing tip and tip of sixth primary (p6; counted from innermost primary outwards); ***3*** colouration of underparts in first-winter birds; ***4*** colouration of underparts in adult females; ***5*** colouration on crown in adult females; ***6*** prominence of dark necklace on breast in adult males; ***7*** extent of white on throat in adult males; and ***8*** extent of a white supercilium in adult males. In addition, the paper deals with song and contact calls of the taxa involved.

Analysis of variation

The morphometrics of interest were obtained from museum specimens. Measurements were taken to the nearest 0.1 mm with calipers, and averages and ranges for geographical regions and taxa were calculated.

For each plumage feature, variation was categorised into four (for the extent of supercilium in males) or three (for all other features) classes (see figure 3, 5, 6, 8, 9 and 11). Then, specimens and birds in field photographs were scored according to these classes, and averages and score frequencies for regions were calculated and compared. The categorisation attempts to capture underlying continuous variation by defining classes that represent the distal ends of variation in each plumage feature as well as intermediate appearances. When scoring individual birds, this inevitably means that a few border cases have to be handled. Also, assessment of colour hues in field photographs can be challenging. Admittedly, the chosen method is

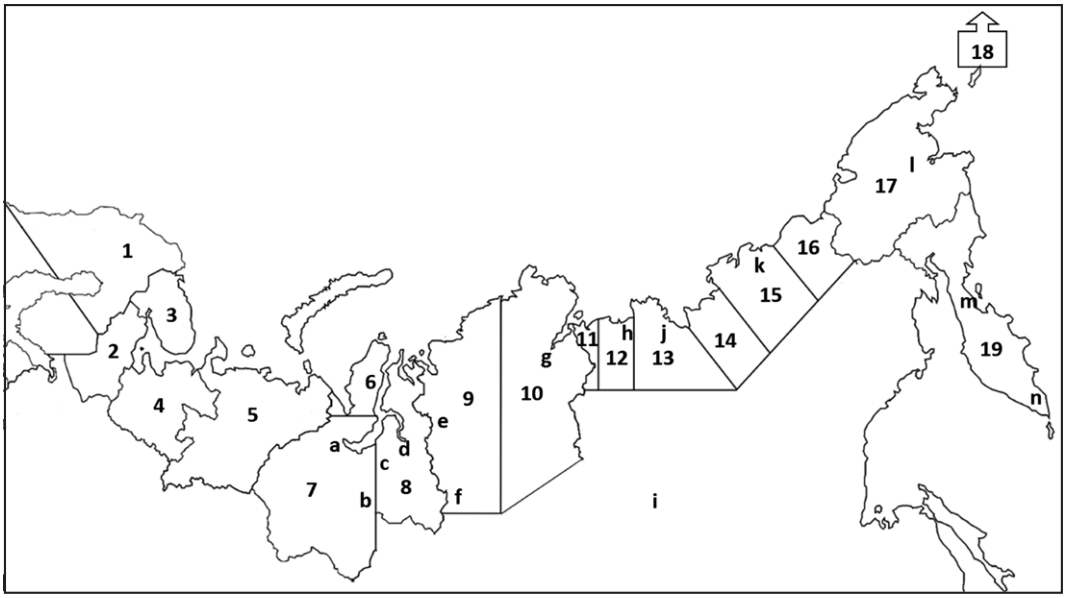

FIGURE 1 Arctic regions referred to in text and figures. Some regions correspond to administrative geographical entities while others have been defined subjectively for purpose of illustrating variation in studied features. **1** Northern Scandinavia; **2** Karelia; **3** Murmansk; **4** Arkhangelsk; **5** Komi & NAO (Nenets Autonomous Okrug); **6** Yamal; **7** Ob river basin; **8** Lower Yenisey and Taz; **9** Western Taimyr; **10** Eastern Taimyr; **11** Lower Anabar; **12** Lower Olenyok; **13** Lower Lena; **14** Lower Yana; **15** Lower Indigirka; **16** Lower Kolyma; **17** Chukotka; **18** Alaska (not shown in map); **19** Kamchatka. Lower case letters denote some specific locations mentioned in text. **a** Labytnangi and Salekhard; **b** Nyabrsk; **c** Novy Urengoy; **d** Tazovsky; **e** Norilsk; **f** Baklanikha river; **g** Khatanga; **h** Taimylyr; **i** Suntarsky district; **j** Tiksi; **k** Chokurdakh; **l** Anadyr; **m** Ossora; **n** Petropavlovsk-Kamchatsky.

thus less precise compared to quantitative tools for plumage analysis that are available when working solely with museum specimens. However, given that the categorisation was applied consistently across the studied sample, it was deemed sufficient for the purpose of identifying large scale patterns of average differences between geographical regions. When estimating significance of average differences between geographical regions and the correlation between plumage features within regions, the Chi-squared (χ^2) and Goodman & Kruskal's gamma statistics were applied, respectively, acknowledging that the classes are better regarded as categorical rather than continuous variables.

In order to detect changes in hind claw length and plumage features over time in Arctic population, averages for old specimens were compared with recently collected specimens and field photographs.

After the moult into adult plumage during the first winter, ageing yellow wagtails is challenging, not least in field photographs and abraded specimens, and after the first complete moult in the first summer the plumage of second calendar-year birds is identical to older birds. Consequently, only a rather small proportion of sampled individuals showing typical characteristics of either second calendar-year birds or older were aged with reasonable certainty, based on assessment of wear to wing coverts and wear and shape of primaries and tail feathers. Possibilities to control for effects of age on the studied features were thus limited but in sample from Northern Scandinavia, differences between age groups are small and not statistically significant.

For vocalisations, qualitative assessments of differences between regions and taxa were made based on sound recordings by the author and others (Veprintsev & Veprintseva 2007, Zöckler 2007; www.hbw.com/ibc, www.macaulaylibrary.org, www.xeno-canto.org,), and on sonagrams of these recordings. Differences in songs were quantified using the software packages Audacity 2.4.2 (Audacity Team) and Raven Lite 2.0 (Cornell Lab of Ornithology), by identifying maximum and minimum frequencies of song notes in sonagrams and estimating average number of notes per second.

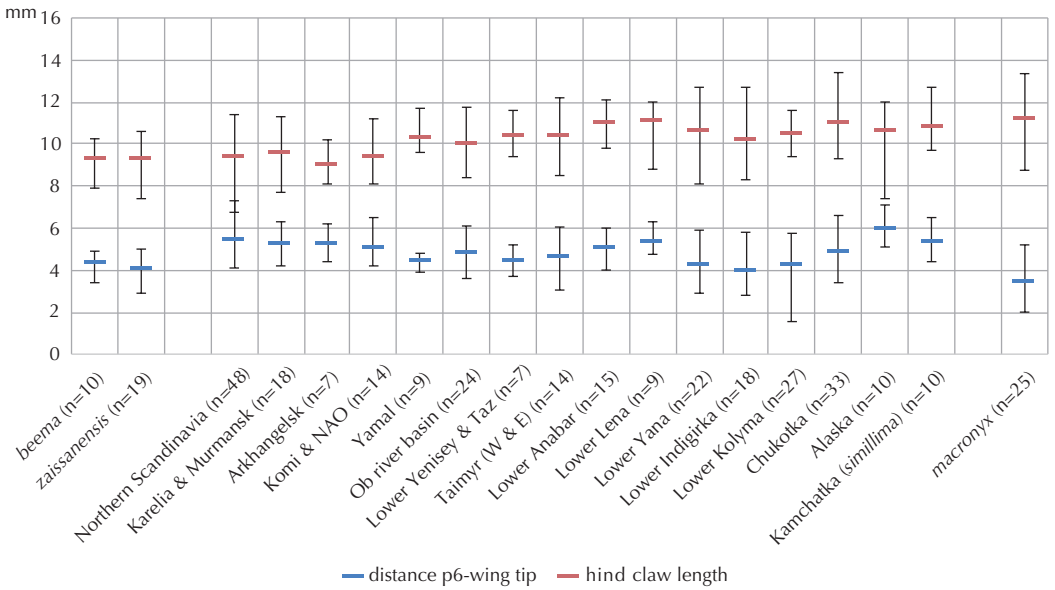

FIGURE 2 Variation in hind claw length and distance between wing tip and p6 in yellow wagtail *Motacilla flava* sensu lato. Bars show sample averages for each region and whiskers show maximum and minimum values. As no significant differences between females and males were found, sexes are pooled. Juvenile and first-winter birds are not included.

Presentation of results

For Arctic yellow wagtail populations, variation in the studied features is presented according to regions defined in figure 1. In cases where a feature was examined in only a small number of specimens/live birds from one region, samples were pooled across regions, as denoted in the figures in the Results section. For morphometrics and plumage, variation in features is presented for Arctic regions, including *simillima* on Kamchatka, Russia, as well as for *beema*, *zaissanensis* and *macronyx*. The three southern taxa are of interest because of plumage similarity to Arctic populations without a supercilium (*macronyx*) and with a supercilium (*beema* and *zaissanensis*). In addition, a comparison between *beema* and *zaissanensis* is of interest as they are similar and breed in close proximity. The initial ambition was to present separate data for *angarensis* as well. However, most examined specimens labelled as *angarensis* could be assigned to Arctic regions or to suspected spring migrants. The *angarensis* type specimen and one paratype collected in the Baikal area, Russia, in June as well as one specimen collected in the Suntarsky district, Russia, in July constitute the only exceptions. They are dealt with under Discussion.

Results

Morphometrics

Variation in hind claw length is slight across the studied range, with longer average measurements from Yamal and the Ob river basin and eastwards in Siberia, Russia, than further west (figure 2). The measurements of *beema* and *zaissanensis* align with Arctic birds west from Yamal, whereas those of *macronyx* align with eastern birds (the same is true for *M t taivana* (hereafter *taivana*); see measurements in Alström & Mild 2003). Comparison of hind claw length between old and recent specimens revealed only small differences in most regions, and no geographical patterns indicating changes in the composition of birds with long versus short hind claws over time were found.

The distance between the wing tip and p6 indicates pointedness of the wing, which is typically associated with migration distance in passerines. Accordingly, measurements of the southern *macronyx*, *beema* and *zaissanensis* are shorter than in Arctic birds (figure 2). The variation across Arctic regions is slight but it does not appear to be random; instead, it might reflect a shorter migration distance in birds breeding between Yamal and Taimyr (probably, these populations migrate at least partly to the Indian subcontinent, see below

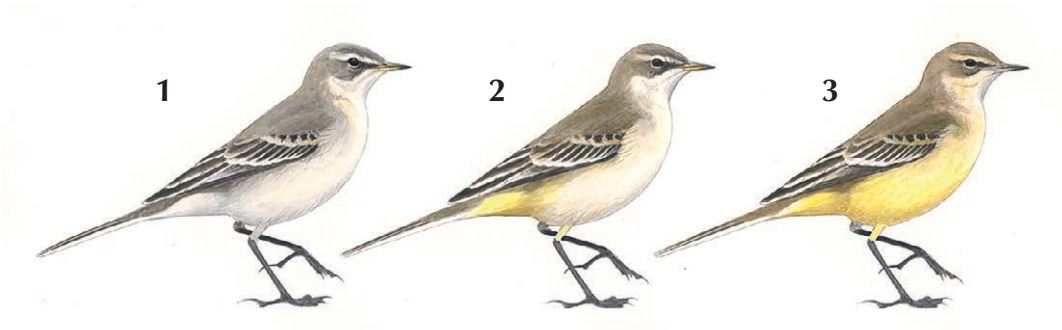

FIGURE 3 Categorisation of amount of yellow in underparts of first-winter birds in yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato *(Hans Larsson)*. **1** No or very little yellow, if present hardly discernible and confined to vent. **2** Limited amount of yellow readily visible but confined to vent and lower belly and flank. **3** At least lower half of belly with strong yellow wash.

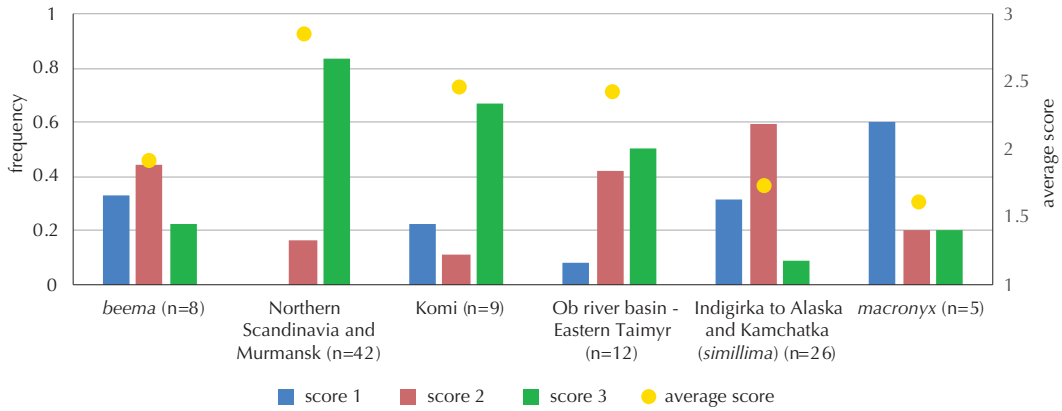

FIGURE 4 Frequency distributions of scores for colouration on underparts in first-winter yellow wagtail *Motacilla flava* sensu lato (bars; left vertical axis) and average scores (yellow dots; right vertical axis).

under Contact calls) and between Lower Yana and Lower Kolyma, respectively. The largest measurements were found in birds from Alaska, USA, presumably reflecting a long migration distance to south-eastern Asia (or even Australia, where some Eastern Yellow Wagtails winter).

Plumage

Figure 4, 7, 10, 12 and 13 show scores for studied plumage features across Arctic regions and in *beema*, *zaissanensis* and *macronyx*, based on the categorisation into classes illustrated in figure 3, 5, 6, 8, 9 and 11. Except for underpart colouration in first-winter birds and extent of supercilium in adult males, the range of variation within regions is not shown, as overlap is complete: all feature classes can be found in all regions, albeit with varying frequency.

Colouration of underparts in first-winter birds

The number of examined first-winter birds that can be attributed to geographical origin with reasonable certainty, ie, collected in August or early September at or close to breeding grounds after having completed post-juvenile moult of underparts, is low for most Arctic regions. Therefore, aggregate average scores and score frequencies for four larger areas are given in figure 4. On average, yellow hues to the underparts decrease eastwards but, in all Arctic regions, it is possible to encounter individuals showing rather extensive yellow. In the sample from Northern Scandinavia and Murmansk, Russia, there is no bird with score 1, ie, with no or only very faint yellow on vent. However, such birds are rare but regular during early autumn migration in southern Sweden and it is reasonable to believe that most of them are *flava* or *thunbergi*

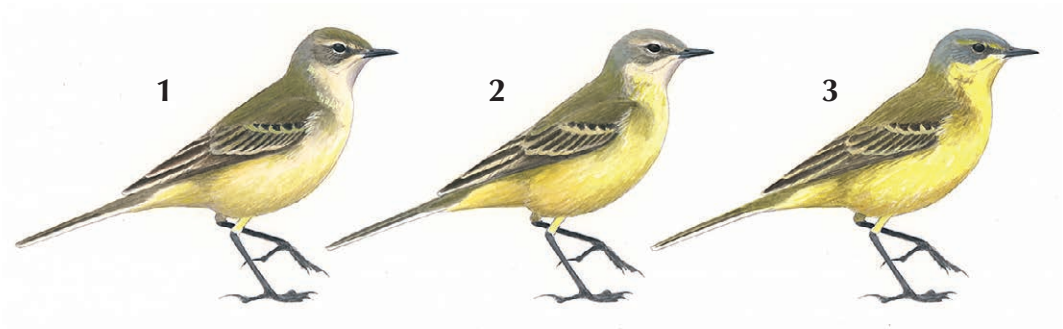

FIGURE 5 Categorisation of colouration of underparts in adult female yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato *(Hans Larsson)*. **1** Prominent yellow confined mainly to belly and lower breast, with upper breast and throat whitish or buffish with only weak yellow cast. **2** Underparts mostly yellow except for throat that is mostly whitish or buffish. **3** Entire underparts including throat yellow.

FIGURE 6 Categorisation of colouration on crown in adult female yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato *(Hans Larsson)*. **1** Crown with obvious green or brown cast, similar to mantle colour (nape is usually greyer). **2** Crown greyer than mantle, with weak or no green, brown or blue cast. **3** Crown bluish grey, clearly contrasting with mantle, similar to colour in many males.

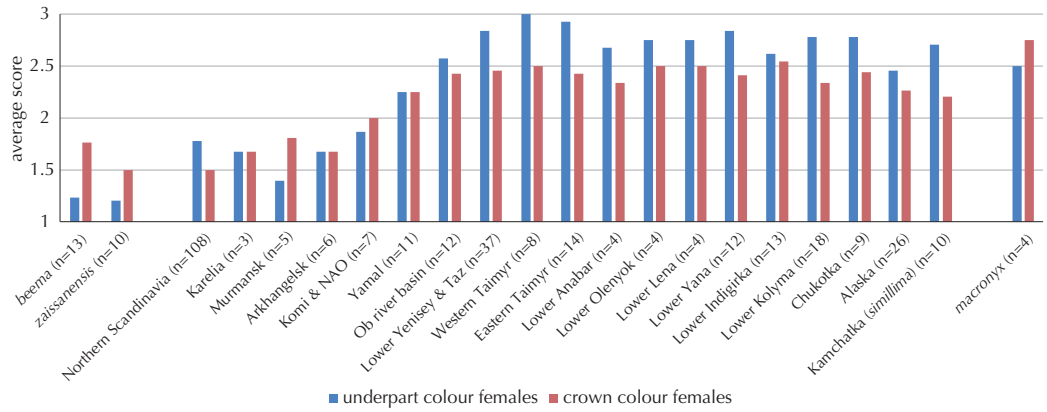

FIGURE 7 Average scores for colouration below and on crown in female yellow wagtail *Motacilla flava* sensu lato

rather than eastern vagrants. *Beema* and *macronyx* are similar in colouration to Arctic birds in eastern Siberia. Only one first-winter *zaissanensis* has been examined (score 2). It seems that yellow hues become fainter in late autumn and winter due to bleaching and abrasion. The amount of yellow below appears to co-vary with mantle colouration in first-winter birds, as birds with no or little yellow below tend to have a greyer mantle without brownish cast. Differences in mantle colour are however subtle and difficult to categorise into classes, and this feature is not considered here.

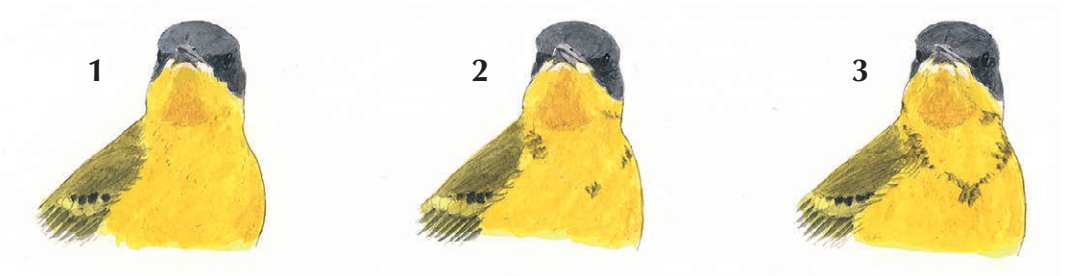

FIGURE 8 Categorisation of prominence of necklace in adult male yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato *(Hans Larsson)*. **1** No or only very few and weak spots on upper breast. **2** Spots on upper breast evident but small and isolated, not forming large patches or complete necklace. **3** Prominent spots forming large patches or complete necklace.

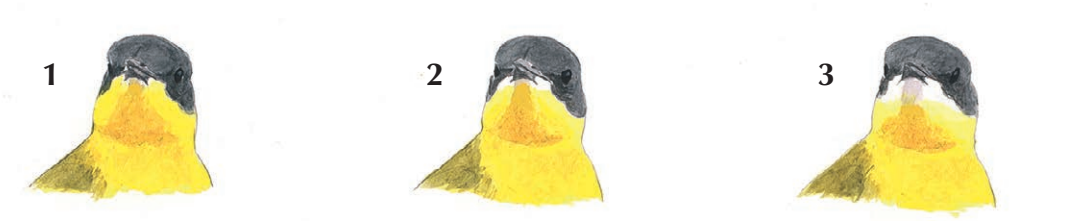

FIGURE 9 Categorisation of extent of white on throat in adult male yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato *(Hans Larsson)*. **1** Throat yellow with at most a few white feathers below bill base. **2** Prominent white below bill and ear coverts but white covering less than half of throat. **3** White covering more than half of throat.

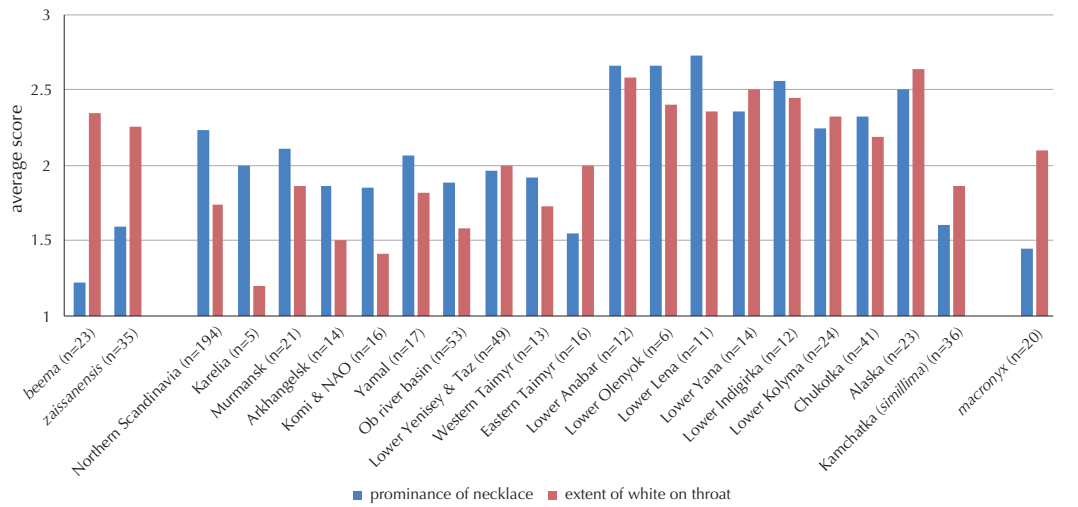

FIGURE 10 Average score for prominence of necklace and extent of white on throat in adult male yellow wagtail *Motacilla flava* sensu lato. Increase in extent of white on throat between Eastern Taimyr and Lower Anabar aligns with results in Sammalisto (1961), who reported more extensive white throats in Yakutia (ie, area between Lower Anabar and Kolyma) compared with Arctic breeders further west in Russia and Scandinavia.

FIGURE 11 Categorisation of extent of supercilium in adult male yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato *(Hans Larsson)*. **1** No supercilium. **2** Very faint and restricted supercilium, often only few white feathers. **3** Thin and/or short supercilium, either only behind or in front of eye or both – in latter case short behind eye. **4** Prominent complete white supercilium both behind and in front of eye.

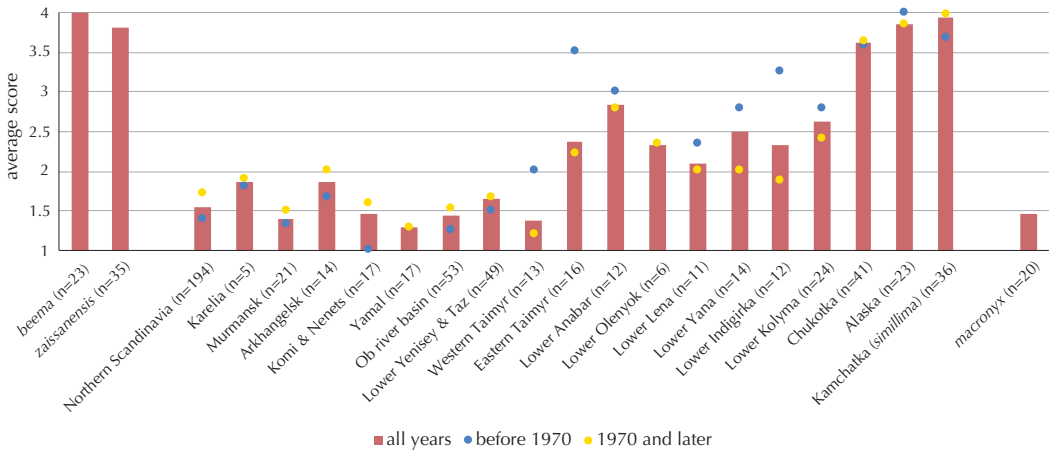

FIGURE 12 Extent of white supercilium in adult male yellow wagtail *Motacilla flava* sensu lato. Bars show average score for total samples from each region. Blue dots show average for specimens collected before 1970, while yellow dots show average for specimens/field photographs collected/taken in 1970 or later.

Colouration of underparts and on crown in adult females

In sampled Scandinavian females that were possible to age, no significant difference in the colouration of underparts was identified between second calendar-year birds (n=10) and older birds (n=13) (χ^2 test; p=0.38). In other regions, the number of birds that are aged with certainty was too low to assess possible differences, and age classes are pooled in figure 7. Average scores for colouration of underparts and crown in adult females increase gradually between Arkhangelsk and the Ob river basin. Here and eastwards, most females show a rather male-like plumage (eg, plate 465), although exceptions occur. *Macronyx* females are generally male-like, whereas *beema* and *zaissanensis* females are duller than males and often greyer above and whiter below than Arctic females (including Northern Scandinavian birds).

Prominence of necklace and extent of white on throat in adult males

In Scandinavian males that could be aged, no significant differences between second calendar-year birds (n=22) and older birds (n=27) were found in terms of prominence of necklace and extent of white on throat (χ^2 test; p=0.23 for prominence of necklace and p=0.63 for extent of white on throat). In most other regions, the number of birds aged with certainty was too low to assess possible differences, and age classes are pooled in figure 10.

In the Arctic regions, birds east of Taimyr show on average more prominent dark necklaces and more extensive white throats than birds in Taimyr and westwards, although average prominence of necklace in Scandinavia, Karelia and Murmansk is similar to that in some regions in eastern Siberia. For both features, differences are statistically significant when comparing the area between Scandinavia and Taimyr with the area between Lower

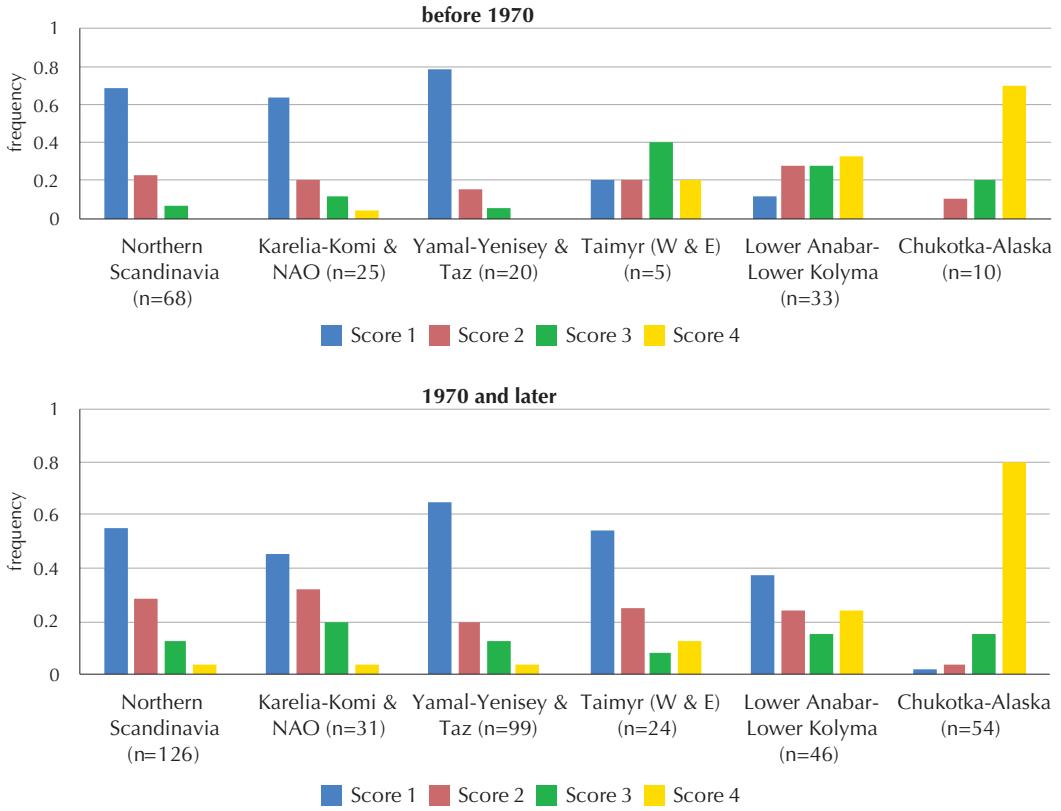

FIGURE 13 Frequency distributions of scores for extent of supercilium in adult male yellow wagtail *Motacilla flava* sensu lato. Upper figure shows old specimens (collected before 1970) and lower figure shows recent specimens/birds in field photographs (collected/taken in 1970 or later). Difference between the two periods suggests increasing share of birds with a short supercilium (score 2-3 in figure 11) over time between Northern Scandinavia and Lower Yenisey and Taz, and increasing share of dark-headed birds (score 1 in figure 11) from Taimyr to Lower Kolyma.

Anabar and Alaska (χ^2 test; $p<0.001$ for both features). Differences are also significant when comparing only the sample from Eastern Taimyr with the sample from Lower Anabar (χ^2 test; $p<0.001$ for both features). Compared with eastern Arctic populations between Lower Anabar and Alaska, both *simillima* and *macronyx* show a significantly cleaner yellow breast on average (χ^2 test; $p<0.001$).

Extent of white supercilium in adult males

Roughly, average scores for extent of white supercilium in males take on three levels across the Arctic: low scores between Scandinavia and Western Taimyr, intermediate scores between Eastern Taimyr and Lower Kolyma, and high scores in Chukotka, Kamchatka and Alaska (figure 12). Across most of the Arctic, dark-headed birds as well as birds with a short or long supercilium can be encountered, although there are no completely dark-headed birds in the samples from Alaska and Kamchatka (*simillima*).

Changes in extent of supercilium in adult males over time

For all examined plumage features except the extent of supercilium in males, comparisons between old specimens and recent specimens and photographs revealed only small differences over time, without clear geographical patterns. For supercilium in males, specimens collected before 1970 have lower average scores (less extensive supercilium) than more recent specimens and birds on photographs between Scandinavia and the Ob river basin, whereas the opposite is true in most regions between Lower Yenisey and Taz and Lower Kolyma, as illustrated with blue and yellow dots in figure 12.

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456 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, first-winter *thunbergi*, Tynderö, central Sweden, 22 August 2017 *(Håkan Sundin)*. Locality situated north of range of *flava*. Individual with extensive yellow below; most common plumage in Scandinavian first-winter birds. Weak supercilium indicates *thunbergi*. **457** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, first-winter *thunbergi*, Öfjärden, northern Sweden, 12 August 2017 *(Dirk van Gansberghe)*. Example of bird with yellow mainly confined to vent. **458** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, first-winter, Selenga, lake Baikal, Russia, 4 September 2009 *(Alexander Hellquist)*. Location, sharp calls and short supercilium suggest eastern dark-headed Arctic bird. Grey and white plumage with only weak yellow suffusion confined to vent is frequent in eastern birds. **459** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, first-winter *tschutschensis*, Saint Paul Island, Alaska, USA, 16 August 2018 *(Sulli Gibson)*. Typical grey and white plumage and prominent supercilium often shown in this subspecies.

In most Arctic regions, samples are too small to allow for firm conclusions regarding changes in average scores over time, and also for a meaningful analysis of changes in score frequency distributions over time. Therefore, score frequency distributions across larger areas of combined regions were compiled for old specimens (collected before 1970) and more recent specimens and birds on photographs (figure 13). These distributions suggest an increasing share of birds with a short supercilium (scores 2 and 3 in figure 11) over time between Northern Scandinavia and Lower Yenisey and Taz, and an increasing share of dark-headed birds (score 1 in figure 11) from Taimyr to Lower Kolyma. This might indicate ongoing introgression between dark-headed populations and populations with a supercilium. However, also for these larger areas sample sizes are too small for firm conclusions and more study is required to establish the significance of any trends.

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460 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, first-winter *tschutschensis*, onboard ship outside North Slope, Alaska, USA, 17 August 2015 *(Bill Schmoker/PolarTREC 2015; courtesy of ARCUS)*. Some first-winter birds may show strong buffish suffusion to underparts as well as brownish cast to upperparts. **461** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, first-winter presumed *beema*, Malikent, southern Kazakhstan, 5 October 2012 *(Alexander Hellquist)*. Grey and white plumage is common in *beema*, similar to that in *tschutschensis*. This bird gave soft calls typical of north-western taxa including *beema*. **462** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female *thunbergi*, Luvenga, Murmansk oblast, Russia, 24 June 2011 *(Yuri Bykov)*. Typical female plumage in Scandinavia and westernmost Russia, with weak yellow on throat and upper breast and drab-grey crown colour. **463** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female *thunbergi*, Alvik, northern Sweden, 20 May 2015 *(Peter Nilsson)*. Occasionally, female plumage resembles that of males also in western populations.

Vocalisations

Song

The main element of the song in Western Yellow Wagtail is a rasping note that falls in pitch, often transcribed as *tsrie* or *zrie*. The song often consists of single notes given at a slow pace but sometimes they are repeated in fast sequences forming phrases, and sometimes they are combined with twittering or squeaky calls. The same individual can alter between these variants. The single-note song type consisting of isolated notes given at a slow pace occurs in all Western Yellow Wagtail subspecies including *zaissanensis* and also in *M f leucocephala* (hereafter *leucocephala*), of which hardly any recordings are available (one is published at www.youtube.com/watch?v=DgXH3HEEqf8). In contrast, none of c 25 singing *tschutschensis*, *simillima* and *macronyx* in examined recordings have used the single-note song type, and it has not been heard among c 30 singing males during field studies in Chukotka, Kamchatka and Alaska. Occasion-

464 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female, Salekhard, Russia, 8 June 2018 *(Alexander Hellquist)*. Drab females like this bird occur throughout Arctic, although they become less frequent from Lower Ob and eastwards. **465** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female, Norilsk, Russia, 8 July 2015 *(Alexander Hellquist)*. In eastern populations, females are regularly very male-like and certain birds are difficult to sex with certainty. This bird was paired with typical dark-headed male. **466** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female, Khatanga, Russia, 10 July 2015 *(Alexander Hellquist)*. Male-like bird with prominent supercilium. **467** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female, Taimylyr, Russia, 6 July 2016 *(Alexander Hellquist)*

ally, notes reminiscent of the single-note song type are given by eastern birds but the contexts of the examined cases indicate that they function as alarm calls (one example from Alaska is available at https://macaulaylibrary.org/asset/131298).

In sound-recorded birds from Chukotka, Kamchatka and Alaska (*tschutschensis* and *simillima*), as well as in *macronyx* and *taivana*, the song consists of rapid sequences of two to 17 ringing high-pitched notes repeated at a pace of 5.6 to 7.9 notes per second: *zri-zri-zri-zri*... The number of notes varies between phrases in the same individual. This fast song type has also been recorded in the Lower Indigirka (Zöckler 2007). Few songs have been examined from north-central Siberia but shorter variants of the fast song type with only two or three notes repeated at a fast pace have been recorded in two birds in Lower Lena, two birds in Lower Olenyok, and one bird in Eastern Taimyr, all in early July. The lower number of notes could reflect geographical variation, but it is also possible that the phrases become shorter as song intensity goes down in summer.

Out of 26 recorded singing Scandinavian *thunbergi* males, seven included phrases consisting of repeated notes. Compared with phrases in eastern

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468 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female, north of Chokurdakh, Russia, 26 June 2019 *(Chris van Rijswijk)*. Paired with male in plate 488. **469** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female, Anapka bay, northern Kamchatka, Russia, 29 June 2009 *(Alexander Hellquist)*. Photograph taken in area where *simillima* and *tschutschensis* meet. **470** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female *zaissanensis*, Kalawu Tekele lake, northern Xinjiang, China, 19 May 2011 *(Alexander Hellquist)*. Limited yellow below and greyish above, similar to many *beema* and *feldegg* females. **471** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female *zaissanensis*, Kalawu Tekele lake, northern Xinjiang, China, 19 May 2011 *(Peter Schmidt)*

birds, these differed in having only two to four notes per phrase, a slower pace of 2.8 to 5.1 notes per second, and a lower minimum frequency of each note (often between 3 and 4 kHz as opposed to 4 and 5 kHz in eastern birds) with a less ringing voice (figure 14 and table 2). In these aspects, they align with the fast-paced song given by a larger studied sample of other Western Yellow Wagtail subspecies including *M f flava* (hereafter *flava*), *M f flavissima* (hereafter *flavissima*), *M f iberiae* (hereafter *iberiae*) and *M f feldegg* (hereafter *feldegg*). In this larger sample, there were birds giving up to six notes per phrase, and in a few the voice was rather high-pitched with a ringing quality. The pace was still lower than in eastern birds, with a maximum of 5.2 notes per second, but in some cases, the overall impression was nonetheless very similar.

In the area between the Ob river basin and Western Taimyr, 10 of 29 singing males recorded in June and July included phrases consisting of repeated notes, while recordings of the remaining 19 birds only included the single-note song type. Birds using the fast song type gave two to six notes per phrase with a pace of 3.1 to 6 notes per second, on average faster than in Scandinavian *thunbergi* but slower than in *tschutschensis* and *simillima*. In most birds, the minimum frequency of each

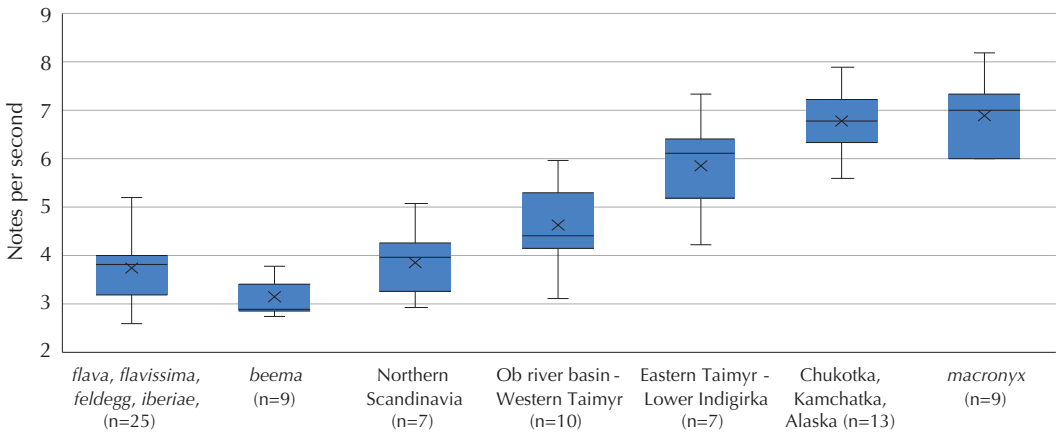

FIGURE 14 Box plot showing variation in pace (number of notes per second) of 'fast song type' in yellow wagtail *Motacilla flava* sensu lato, ie, song phrases consisting of two or more notes. For recordings containing multiple phrases from one individual, averages from three phrases are used. Details of just two examined *zaissanensis* not shown here but detailed in table 2. Boxes outline first to third quartiles, with middle line denoting median value and cross mark denoting average value. Whiskers denote maximum and minimum value.

TABLE 2 Pace, minimum frequency and maximum number of notes per phrase in the 'fast song type' in yellow wagtail *Motacilla flava* sensu lato, ie, song phrases consisting of two or more notes. For recordings containing multiple phrases from one individual, pace and minimum frequency are calculated as average of three phrases.

	Number of notes per second (average and range across recorded individuals)	Minimum frequency (kHz) (average and range across recorded individuals)	Maximum number of notes per phrase (average and range across recorded individuals)	Number of recorded phrases/ individuals
flava, flavissima, feldegg and *iberiae*	3.8 (2.6-5.2)	3.8 (2.8-5.0)	4.0 (2-6)	191/25
beema	3.1 (2.7-3.7)	3.8 (2.8-5.5)	2.2 (2-3)	39/9
zaissanensis	4.5 (3.8-5.2)	4.1 (3.7-4.5)	3.0 (2-4)	20/2
Northern Scandinavia	3.9 (2.9-5.1)	3.3 (2.7-4.0)	2.7 (2-4)	41/7
Ob river basin – Western Taimyr	4.6 (3.1-6.0)	4.4 (3.0-5.0)	4.4 (2-9)	112/10
Eastern Taimyr – Lower Indigirka	5.8 (4.2-7.4)	4.9 (4.2-5.5)	3.4 (2-8)	30/7
Chukotka, Kamchatka, Alaska	6.8 (5.6-7.9)	4.6 (3.5-5.6)	9.0 (3-17)	180/13
macronyx	6.9 (6.0-8.2)	4.9 (3.5-6.2)	6.0 (3-16)	79/9

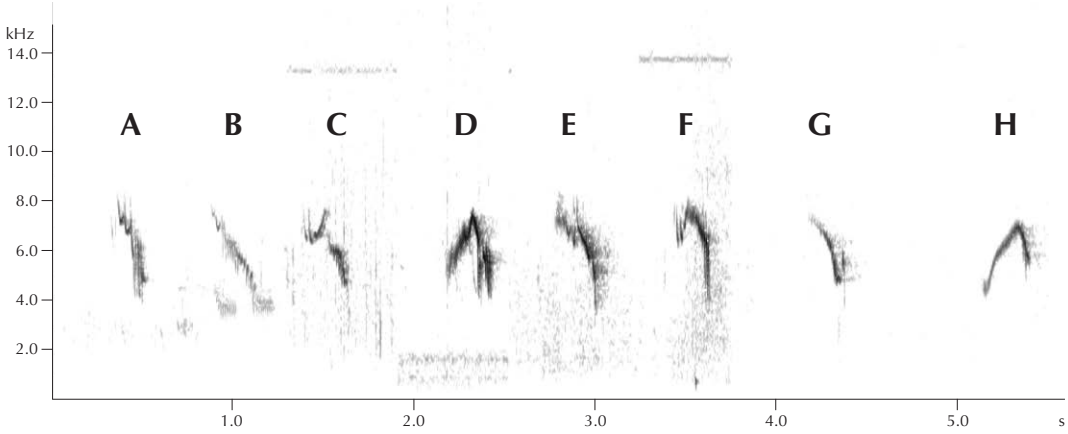

FIGURE 15 Song of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of single-note song type. **A** migrating *thunbergi*, Gotland, southern Sweden, 10 May 2014 *(Alexander Hellquist)*. **B** migrating *thunbergi*, Gotland, southern Sweden, 8 May 2016 *(Alexander Hellquist)*. **C** dark-headed male, Salekhard, Russia, 8 June 2018 *(Alexander Hellquist)*. **D** dark-headed male, Salekhard, Russia, 7 June 2018 *(Alexander Hellquist)*. **E** dark-headed male (plate 481), Tazovsky, Russia, 6 July 2017 *(Alexander Hellquist)*. **F-H** dark-headed male, Norilsk, Russia, 12 June 2018 *(Alexander Hellquist)*.

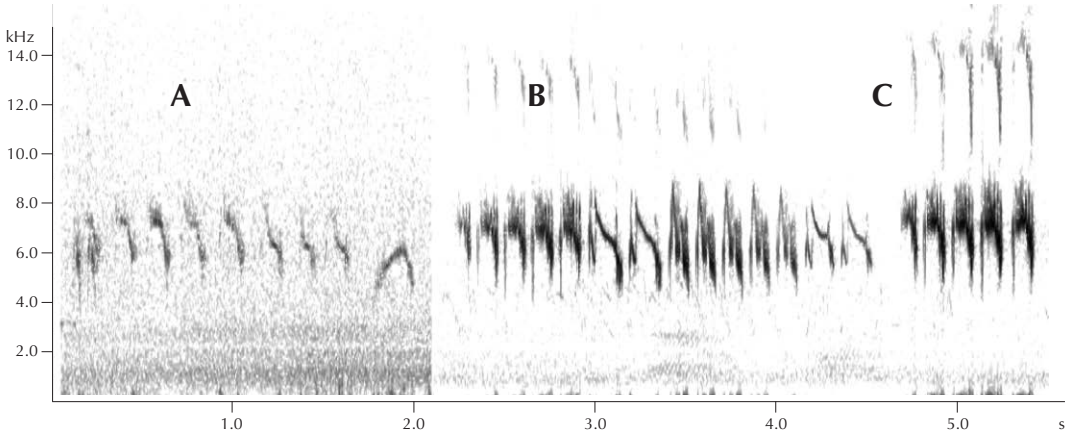

FIGURE 16 Song of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of fast song type from eastern Siberia, Russia. **A** male, Ossora (area where *simillima* and *tschutschensis* meet), 14 June 2009 *(Alexander Hellquist)*. **B-C** two phrases from *simillima*, Petropavlovsk-Kamchatsky, 12 June 2009 *(Alexander Hellquist)*. As evident in A and B, there are often alterations in appearance of notes within phrases.

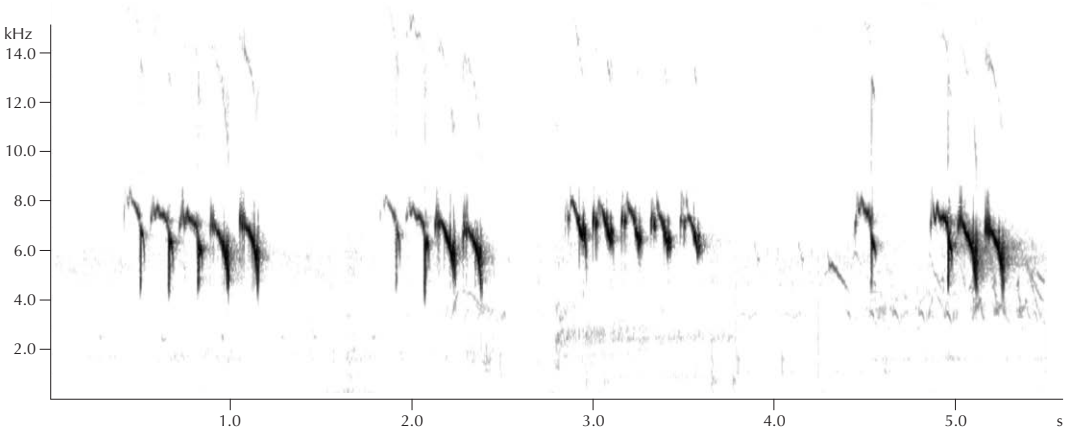

FIGURE 17 Song of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Four fast song type phrases from male, Nome, Alaska, USA, 26 June 2015 *(Bob Mcguire)*.

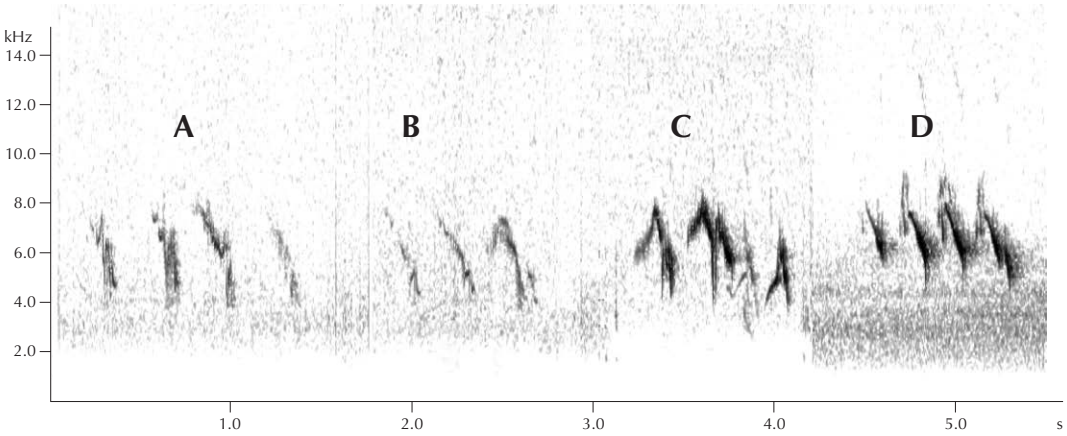

FIGURE 18 Song of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of fast song type in Scandinavia and western Siberia, Russia. **A** migrating *thunbergi*, Gotland, southern Sweden, 10 May 2014 *(Alexander Hellquist)*. **B** migrating *thunbergi*, Gotland, southern Sweden, 8 May 2016 *(Alexander Hellquist)*. **C** male with weak supercilium (plate 480), Salekhard, Russia, 7 June 2018 *(Alexander Hellquist)*. **D** dark-headed male, Norilsk, Russia, 12 June 2018 (plate 484) *(Alexander Hellquist)*. On average, pace of fast song type is higher in western Siberia than in Scandinavia.

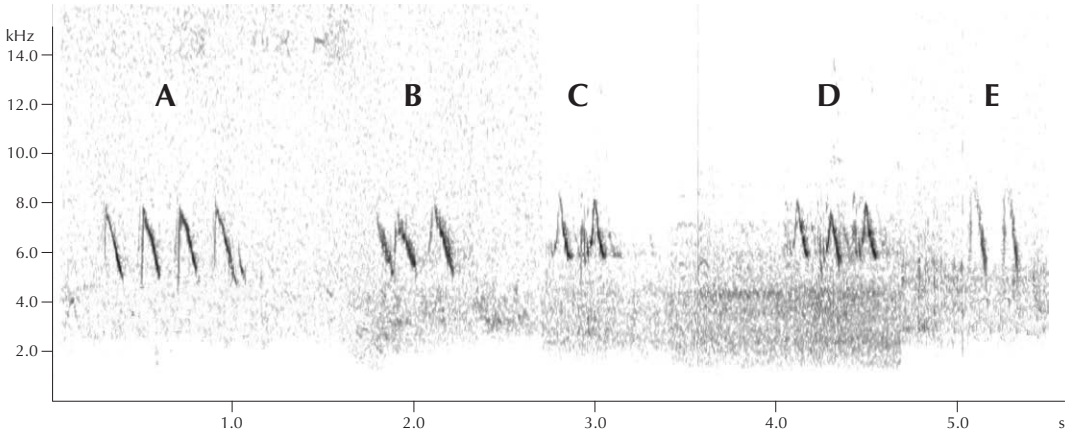

FIGURE 19 Song of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of simple variants of presumed fast song type, consisting of rapid sequences of call-like notes. **A** migrating *thunbergi*, Gotland, southern Sweden, 8 May 2016 *(Alexander Hellquist)*. **B** dark-headed male, Salekhard, Russia, 7 June 2018 *(Alexander Hellquist)*. **C-D** two phrases from dark-headed male, Khatanga, Russia, 9 July 2015 *(Alexander Hellquist)*. **E** male with short supercilium, Taimylyr, Russia, 13 July 2016 *(Alexander Hellquist)*. Similar song has also been recorded in Lower Indigirka (Zöckler 2007).

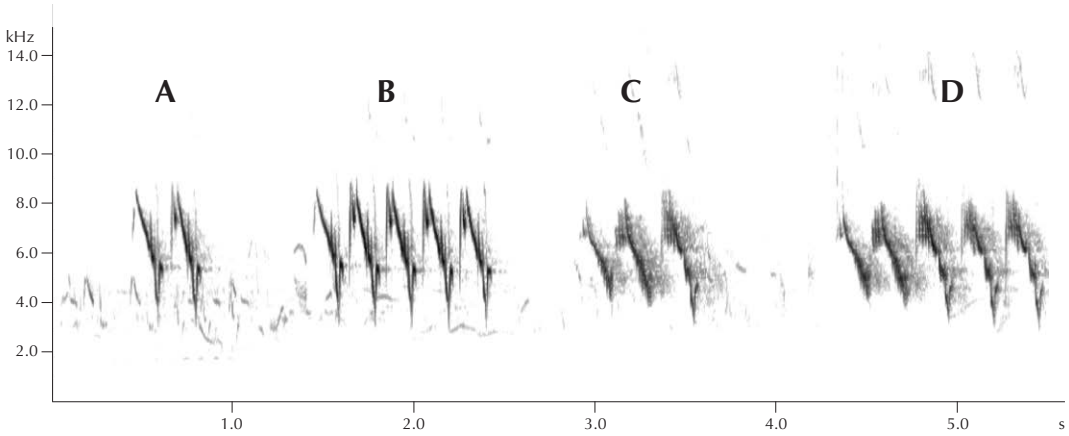

FIGURE 20 Song of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of fast song type in western birds that approach pace of song in eastern birds. **A-B** two phrases from bird not labelled to subspecies (based on location either *thunbergi* or *flava*), Dvietes Paliene, southern Latvia, 16 June 2012 *(Edmunds Racinskis)*. **C-D** two phrases from nominate *flava*, gmina Szreńsk, central Poland, 14 June 2016 *(Piotr Szczypinski)*. With c 5 notes per second, these phrases match pace of many examined recordings from central Siberia east to Lower Indigirka but they are still slower than sampled *tschutschensis* and *simillima*. Minimum frequency of notes is around 3 kHz, which is lower than sampled birds east of Taimyr.

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472 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, female *zaissanensis*, Kalawu Tekele lake, northern Xinjiang, China, 17 May 2011 *(Petter Haldén)*. Bird with olive cast above and slightly stronger yellow cast below. **473** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *thunbergi*, Stordalen, northern Sweden, 17 June 2016 *(Daniel Pettersson)*. Typical bird. **474** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *thunbergi*, Karigasniemi, northern Finland, 3 June 2017 *(Daniel Pettersson)*. Example of Scandinavian male with short supercilium. **475** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *thunbergi*, Stordalen, northern Sweden, 17 June 2017 *(Benny Modig)*. Example of male with blackish crown. C 5% of Arctic birds are as dark as this or even darker, occasionally approaching appearance of *feldegg*, in particular when worn. Easternmost examined bird with blackish crown was collected in Lower Indigirka.

note was similar to that in eastern birds (between 4 and 5 kHz). Among the 10 birds giving the fast song type, six also gave the single-note song type interchangeably.

Contact calls

As pointed out in Alström & Mild (2003) and Bot et al (2014), there are differences in the typical contact calls between Western Yellow Wagtail and the Eastern Yellow Wagtail subspecies *tschutschensis*, *simillima*, *macronyx* and *taivana*. The Western Yellow subspecies *flava*, *flavissima*, *thunbergi*, *beema, leucocephala* and *M f lutea* (hereafter *lutea*) typically give soft calls without prominent *r*-sound: *pslie*, *sliu* or similar. The other Western Yellow subspecies also use these soft calls but also harsher variants with an obvious *r*-sound. In contrast, the typical call in *tschutschensis*, *simillima*, *macronyx* and *taivana* is a sharp rasping *srie*, with a prominent *r*-sound, very similar to calls of Citrine Wagtail *M citreola*. Along the Arctic regions between Scandinavian *thunbergi* and *tschutschensis*, shifts in the

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476 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *thunbergi*, Alvik, northern Sweden, 11 May 2010 *(Peter Nilsson)*. Example of male with prominent supercilium. Such birds occur occasionally in Northern Scandinavia; it is possible that they indicate influence from *flava*. **477** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, south-eastern Komi Republic, Russia, 10 July 2014 *(Nikolay Neufeld)* **478** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, south-eastern Komi Republic, Russia, 14 June 2015 *(Nikolay Neufeld)*. Example of bird with prominent supercilium. Population in Komi may be under influence from *flava* or westernmost *beema* but introgression from eastern Arctic forms is also conceivable. **479** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Salekhard, Russia, 7 June 2018 *(Alexander Hellquist)*. Bird with weak supercilium that gave both single-note song and phrases consisting of two and three notes repeated at fast pace (sonagram figure 18C).

typical call types are apparent. The pattern formed by these shifts is somewhat intricate, and further studies are needed to establish the geographic variation of the involved calls in more detail.

Starting from *tschutschensis* in the Bering Strait region and moving westwards to Lower Olenyok, all studied birds predominantly used sharp calls, seemingly without geographical variation. In most calls, but not all, the *r*-sound was prominent. It was often most conspicuous at the end of the call, with the last descending part in sonagrams becoming wider towards the end as modulations become stronger (figure 22). In Khatanga in Eastern Taimyr, c 500 km west from Lower Olenyok, a first shift in calls is apparent. From here and westwards, calls are not as sharp as typical calls further east, lacking an obvious *r*-sound. Between Khatanga and westwards to at least the Taz peninsula and Novy Urengoy, most calls are still noticeably sharper than typical calls given by Scandinavian *thunbergi*, and representations in sonagrams are similar to those from further east, with a steep ascending onset connected at the top with a longer descending part (figure 23). Compared with calls further east,

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480 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Tazovsky, Russia, 4 July 2017 *(Alexander Hellquist)*. Note prominent dark necklace. This bird gave calls with weak frequency dip in middle (sonagram figure 26D). **481** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Tazovsky, Russia, 6 July 2017 *(Alexander Hellquist)*. This bird gave a single note song (sonagram figure 15E). When not singing, birds with this appearance in central and eastern Siberia can be very difficult to sex with certainty, as females are frequently male-like and often show faint supercilium. Many males show blackish loral area but not all. **482** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Tazovsky, Russia, 6 July 2017 *(Alexander Hellquist)*. This bird gave calls that were similar to those in dark-headed birds in same area, with weak frequency dip in middle (sonagram figure 26E). **483** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Norilsk, Russia, 12 June 2018 *(Alexander Hellquist)*. This bird gave fast song type at moderate pace typical of recorded birds between Ob river basin and Western Taimyr (sonagram figure 18D).

the descending part is often thinner with less pronounced modulations, reflecting the lack of *r*-sound, and in many calls, the second descending part does not widen towards the end. However, some sonagrams are nearly identical to those from eastern birds, even though the difference in terms of *r*-sound can be readily discerned when listening to the recording. Between Khatanga and Lower Olenyok, yellow wagtails occur at least along Lower Anabar but no recordings have been found from that region.

Moving further west, in the Ob river basin and on Yamal, many recorded calls start approaching those of Scandinavian *thunbergi*, although sharper calls similar to those in Taimyr were also given. Only four recordings of calls have been studied from the area between the Ob river basin and Scandinavia: one from the northern Urals (Veprintsev & Veprintseva 2007), one from the Lower Pechora River (www.xeno-canto.org/377981) and two from Karelia (www.xenocanto.org/513495 and www.xeno-canto.org/513497). They all included soft calls.

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484 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Khatanga, Russia, 10 July 2015 *(Alexander Hellquist)*. Bird with prominent supercilium carrying food for nestlings. It gave calls that were similar to those of dark-headed birds in same area, with pronounced frequency dip in middle (sonagram figure 25E). **485** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Khatanga, Russia, 10 July 2015 *(Alexander Hellquist)*. Example of bird with green cast to crown and yellow feathers above eye. This occurs regularly in many yellow wagtail taxa but normally it is more conspicuous when plumage fresh in autumn and early spring. In this case, influence from *taivana* can perhaps not be ruled out, although it would be surprising, given distance between Khatanga and nearest known breeding areas of *taivana* north of lake Baikal. **486** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Taimylyr, Russia, 6 July 2016 *(Alexander Hellquist)*. East of Taimyr, prominent dark necklaces, as in this bird, become more frequent. **487** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Taimylyr, Russia, 13 July 2016 *(Alexander Hellquist)*. This bird gave sharp calls, typical of birds east of Taimyr (sonagram figure 22B).

In *thunbergi* in Scandinavia and Karelia, typical calls are soft and often, but not always, slightly disyllabic, with the ascending and descending parts separated in sonagrams (figure 24). Sharper calls similar to those in Taimyr are occasionally given, just as in other western subspecies including *beema* but they are seemingly never as Citrine Wagtail-like as further east. Conversely, it seems that soft disyllabic calls are rare or absent in Arctic populations east of Taimyr. Soft calls that are similar to typical Scandinavian calls have however been found in one recording of *taivana* (www.xeno-canto.org/489792) and two recordings of *macronyx* (www.xeno-canto.org/144522 and www.xeno-canto.org/144524).

To complicate matters, an additional call type that is distinct from those described above occurs in recordings from the area between Eastern Taimyr (Khatanga) and the Ob river basin (Salekhard) and Yamal. It is characterised by a more complex variation in pitch, with a frequency dip in the middle (figure 25). As in the other calls given in this area,

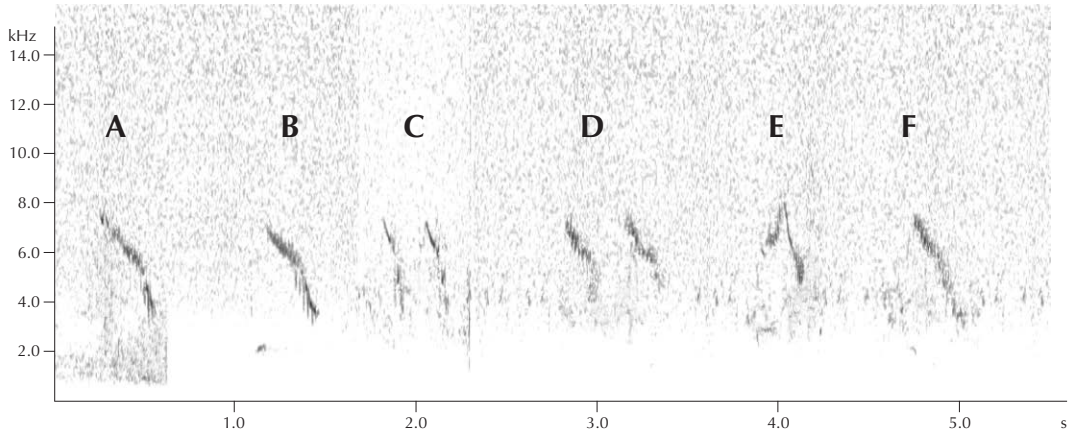

FIGURE 21 Song of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of phrases from the only three sampled singing *zaissanensis*, all recorded at Kalawu Tekele lake (47°01'N 89°45'E), northern Xinjiang, China. **A-B** single-note phrases, 18 May 2011 (time between notes is compressed) *(Alexander Hellquist)*. **C** two-note phrase, 19 May 2011 *(Alexander Hellquist)*. **D-F** one two-note phrase and two single-note phrases (time between phrases compressed), 19 May 2011 *(Alexander Hellquist)*. Songs align with those of Western Yellow Wagtails *M flava*, with pace of two two-note phrases C and D being around 5.2 and 3.8 notes per second, respectively.

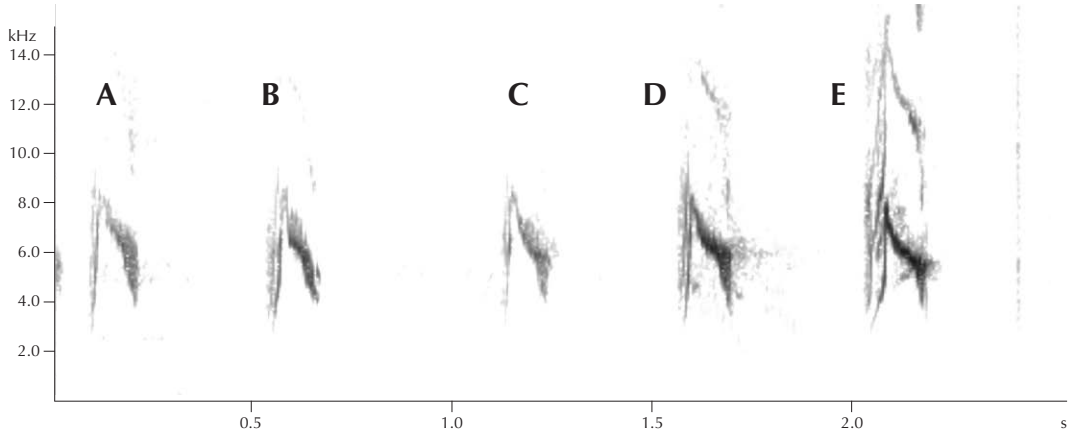

FIGURE 22 Calls of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of typical calls with readily discernable *r*-sound from Lower Olenyok eastwards to Bering Strait. **A** dark-headed male, Taimylyr, Russia, 6 July 2016 *(Alexander Hellquist)*. **B** male with supercilium (plate 487), Taimylyr, Russia, 13 July 2016 *(Alexander Hellquist)*. **C** dark-headed male, Tiksi, Russia, 4 July 2016 *(Alexander Hellquist)*. **D** male *simillima* (plate 491), Petropavlovsk-Kamchatsky, Russia, 11 June 2009 *(Alexander Hellquist)*. **E** female *simillima*, Petropavlovsk-Kamchatsky, Russia, 12 June 2009 *(Alexander Hellquist)*. Note how descending part of sonagram widens towards end (not evident in call B).

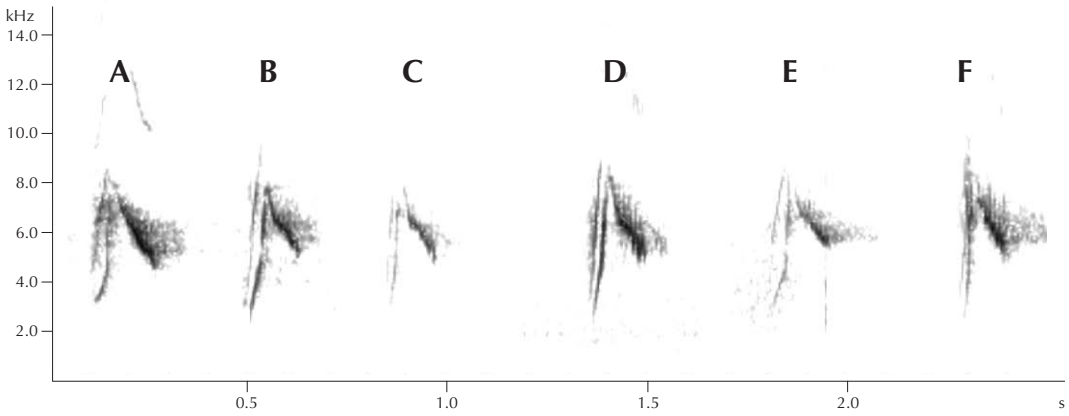

FIGURE 23 Calls of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of rather sharp calls lacking obvious *r*-sound. Such calls occur throughout the Arctic, but they seem most frequent between Taimyr and Yamal/Ob river basin and much less common in Scandinavian *thunbergi* and in *tschutschensis* and *simillima*. **A** male, Porsanger, northern Norway, 11 July 2015 *(Stein Ø Nilsen)*. **B** dark-headed male, Salekhard, Russia, 7 June 2018 *(Alexander Hellquist)*. **C** male with short supercilium, Tazovsky, Russia, 5 July 2017 *(Alexander Hellquist)*. **D** male, Nyabrsk, Russia, 22 June 2009 *(Herman van Oosten)*. **E** female, Norilsk, Russia, 12 June 2018 *(Alexander Hellquist)*. **F** dark-headed male, Khatanga, Russia, 9 July 2015 *(Alexander Hellquist)*. Sonagrams similar to those in figure 22 but modulations less prominent and descending part not widening as clearly as in typical calls east of Taimyr. Note differences in spacing between two bars that constitute first ascending part. In Scandinavia, space is normally wide, while east of Taimyr it is narrow, as described by Bot et al (2014). Between Lower Ob and Western Taimyr, there seems to be considerable variation.

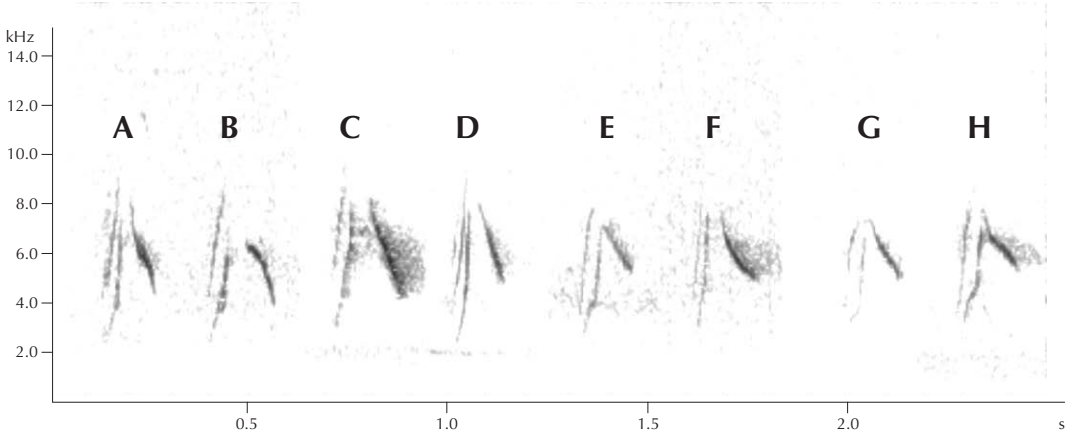

FIGURE 24 Calls of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of soft calls that are typical of Scandinavian *thunbergi* but regularly given in Arctic populations east to Taimyr. **A** migrating male, Gotland, southern Sweden, 7 May 2016 *(Alexander Hellquist)*. **B** migrating male *thunbergi*, Gotland, southern Sweden, 12 May 2012 *(Alexander Hellquist)*. **C** *thunbergi* of unknown sex, Tromsö, northern Norway, 23 May 2014 *(Stein Ø Nilsen)*. **D** female, Salekhard, Russia, 8 June 2018 *(Alexander Hellquist)*. **E** male with short supercilium, Salekhard, Russia, 7 June 2018 *(Alexander Hellquist)*. **F** female, Salekhard, Russia, 8 June 2018 *(Alexander Hellquist)*. **G** female, Norilsk, Russia, 12 June 2018 *(Alexander Hellquist)*. **H** dark-headed male, Norilsk, Russia, 12 June 2018 *(Alexander Hellquist)*. In many calls, gap between ascending and descending part creates disyllabic impression. Note variation in spacing between bars in ascending part.

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488 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, north of Chokurdakh, Russia 26 June 2019 *(Chris van Rijswijk)*. Paired with female in plate 468. **489** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *tschutschensis*, Anadyr, Russia, 3 June 2010 *(Alexander Hellquist)*. Typical bird. **490** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Anadyr, Russia, 7 June 2010 *(Lars Jonsson)*. Dark-headed bird illustrating that this phenotype occurs also in core range of *tschutschensis*, although it has not been found in studied sample from Alaska, USA. **491** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *simillima*, Petropavlovsk-Kamchatsky, Russia, 11 June 2009 *(Alexander Hellquist)*. Individual birds in Kamchatka seem impossible to separate from *tschutschensis* and other Arctic birds with supercilium based on plumage, although males are cleaner yellow below on average. This bird gave sharp calls with conspicuous *r*-sound (sonagram figure 22D).

it lacks *r*-sound while still being sharper than typical calls in Scandinavian *thunbergi*. It seems that it is given more frequently late in the breeding season – possibly, it serves partly as an alarm call. In recordings made in early July in Khatanga, Norilsk, Tazovsky and Novy Urengoy, it was as frequent as the calls described above, while it was much less frequent in early and mid-June among birds recorded in Norilsk and Salekhard. However, recordings of the same call type from spring migrants in Central Asia and from wintering birds in India (figure 28) show that it is used year-round. The most distinct variant of this call type, with a pronounced frequency dip in the middle, seems to be given mainly by populations in Taimyr. Further west, from the Taz peninsula to the Ob river basin and Yamal, most birds give variants with a less pronounced frequency dip (figure 26) that thus become more similar to the calls illustrated in figure 23. However, some birds recorded as far west as Yamal gave calls that are as distinctive as those in Taimyr (eg, figure 25A).

Based on recordings of five individuals and field observations of a few additional birds on breeding

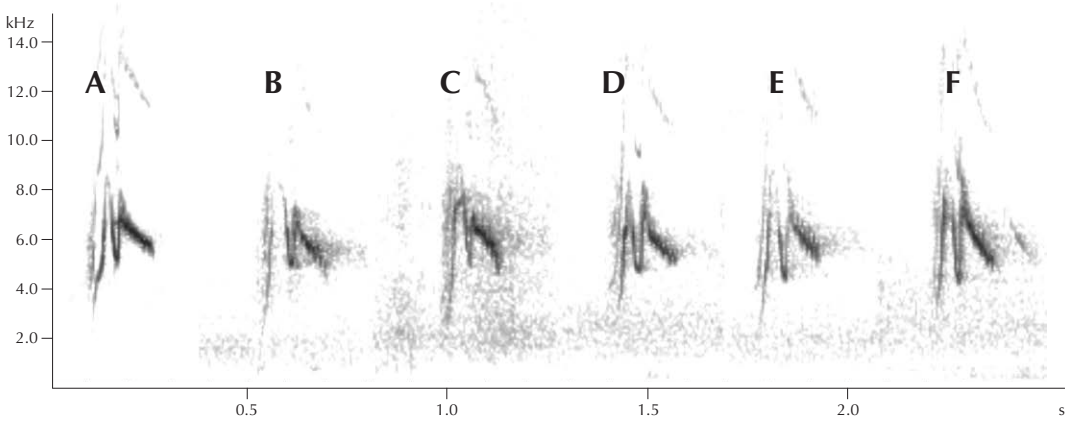

FIGURE 25 Calls of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of calls with pronounced frequency dips in middle, typical, possibly even diagnostic, of breeders between Yamal/Ob river basin and Taimyr. **A** male, southern Yamal, Russia, 10 June 2015 *(Giovanni Boano)*. **B** dark-headed male, Novy Urengoy, Russia, 8 July 2017 *(Alexander Hellquist)*. **C** female, Tazovsky, Russia, 7 July 2017 *(Alexander Hellquist)*. **D** dark-headed male, Norilsk, Russia, 8 July 2015 *(Alexander Hellquist)*. **E** male with prominent supercilium (plate 484), Khatanga, Russia, 10 July 2015 *(Alexander Hellquist)*. **F** male with weak supercilium, Khatanga, Russia, 10 July 2015 *(Alexander Hellquist)*.

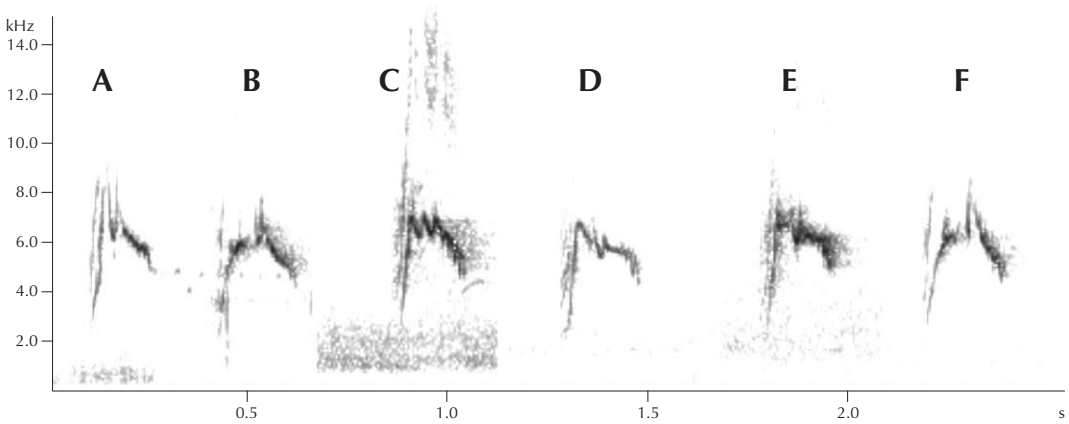

FIGURE 26 Calls of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of calls from area between Yamal and Western Taimyr. Compared with calls in figure 25, these have less pronounced or only vestigial frequency dips in middle. This call type is common in this area but is not diagnostic as similar calls can be given in both Northern Scandinavia and further east. **A** male, southern Yamal, Russia, 7 June 2015 *(Giovanni Boano)*. **B** female, Salekhard, Russia, 7 June 2018 *(Alexander Hellquist)*. **C** dark-headed male, Novy Urengoy, Russia, 8 July 2017 *(Alexander Hellquist)*. **D** dark-headed male (plate 480), Tazovsky, Russia, 4 July 2017 *(Alexander Hellquist)*. **E** male with supercilium (plate 482), Tazovsky, Russia, 6 July 2017 *(Alexander Hellquist)*. **F** dark-headed male, Norilsk, Russia, 12 June 2018 *(Alexander Hellquist)*.

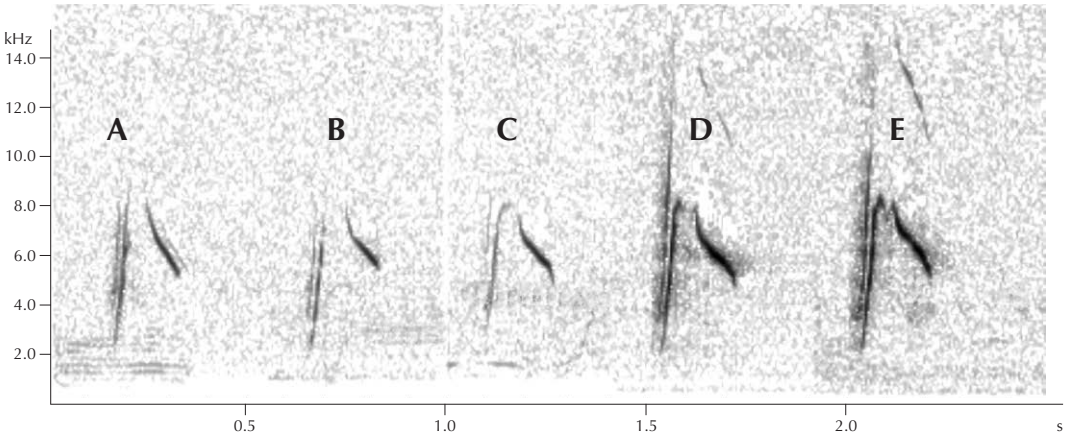

FIGURE 27 Calls of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of calls in three different *zaissanensis*, all from Kalawu Tekele lake, northern Xinjiang, China. **A** male, 18 May 2011 *(Alexander Hellquist)*. **B** male, 18 May 2011 *(Alexander Hellquist)*. **C-E** three calls from male (plate 499), 19 May 2011 *(Alexander Hellquist)*. Calls similar to typical calls in Scandinavian *thunbergi* and in *beema*. Note narrow spacing between bars in ascending part in this small sample, unlike in typical Scandinavian *thunbergi* calls. *Beema* calls seem variable in this respect.

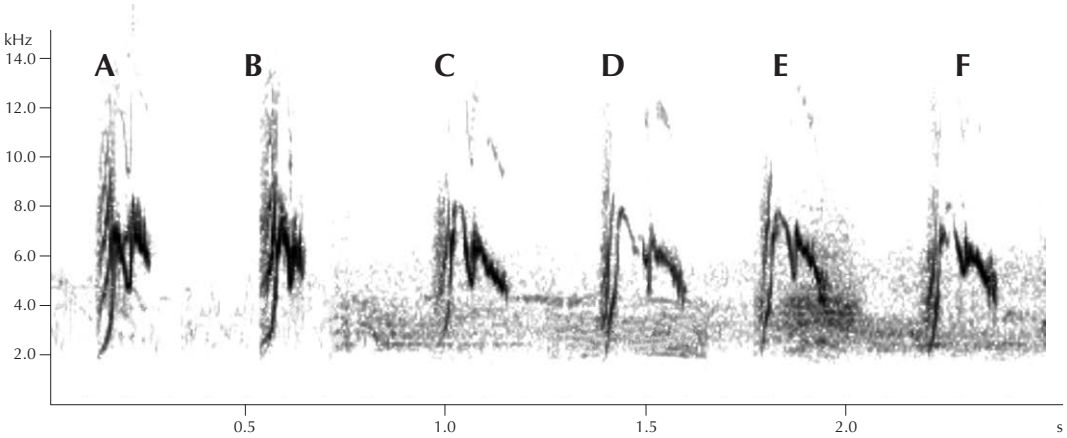

FIGURE 28 Calls of yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato. Examples of calls from wintering and migrating birds matching calls with prominent frequency dips in middle given between Yamal/Ob river basin and Taimyr. **A-B** bird identified as *thunbergi*, south-west of Astana, Kazakhstan, 15 May 2013 *(Thijs Fijen)*. **C-F** bird identified as *thunbergi*, Periyar Tiger Reserve, Kerala, India, 13 April 2017 *(Peter Boesman)*.

grounds in the Altai mountains, Xinjiang, China, it seems that *zaissanensis* consistently give soft calls that are often disyllabic (figure 27).

As yellow wagtail vocalisations are variable and plastic throughout the range, caution is needed when assessing the origin of single individuals based on calls. Recording distance and microphone sensitivity may influence both impression and appearance of vocalisations, with distant calls becoming thinner in sonagrams. Eastern birds may give call variants without a discernible *r*-sound along with typical sharp calls. Conversely, although calls with obvious *r*-sounds have not been encountered in recordings of Scandinavian *thunbergi* from the breeding grounds, migrating birds in southern Sweden occasionally give calls with discernible *r*-sounds. These are rarely if ever as harsh as in birds from eastern Siberia, instead often appearing more similar to short song phrases in sonagrams. A discussion by Martin Garner on rasping

calls from migrants along with sonagrams that are similar to song phrases can be found at https://tinyurl.com/zvkapss. Apart from the proper contact calls described above, all populations of yellow wagtails can produce various short notes that are usually soft, as well as different chirping calls. Keeping these caveats in mind, it seems that birds that consistently give Citrine Wagtail-like calls with prominent *r*-sounds can be identified with reasonable confidence as originating east of Taimyr (southern Western Yellow Wagtail taxa that give calls with prominent *r*-sounds can in most cases be ruled out based on a less sharp, more rolling voice and different appearance of sonagrams; see Bot et al 2014). Furthermore, it is possible that calls with a pronounced frequency dip in the middle are diagnostic of populations breeding in Taimyr and westwards to the Ob river basin/Yamal. The less distinct variants of this call, that are common among breeders between the Taz peninsula and the Ob river basin/Yamal, do not seem to be diagnostic, as they can be matched by occasional calls in Scandinavian *thunbergi* and in birds from east of Taimyr as well as in other yellow wagtail taxa.

This study did not include a thorough analysis of calls given on wintering grounds but 36 examined recordings from southern Thailand and eastwards in south-eastern Asia all contain sharp calls that are consistent with those given by breeding Arctic birds east of Taimyr and by *macronyx* and *taivana* (www.hbw.com/ibc, www.macaulaylibrary.org; www.xeno-canto.org; own recordings). From southern and western India (Kerala, Goa, Maharashtra and Gujarat), 10 recordings labelled as *thunbergi* have been examined (www.hbw.com/ibc, www.macaulaylibrary.org; www.xeno-canto.org; own recordings). Four of these included calls with frequency dips that are typical of breeders between Taimyr and Ob river basin/Yamal (one example in figure 28C-F), while the other six included rather sharp calls without obvious *r*-sounds that also match those of breeders from this area. No recordings labelled as *thunbergi* have been found from sub-Saharan Africa, where most Scandinavian birds are believed to winter. 12 checked unlabeled recordings from sub-Saharan Africa (www.xeno-canto.org) contained soft calls consistent with those of breeders in northern Europe, while the other recordings contained calls that fit either *feldegg* or other south-western taxa.

Correlation between features within regions

Strong correlations between morphometrics, plumage feature scores and vocalisations among birds within single regions in the Arctic could indicate that different populations occur in close proximity or sympatry while maintaining distinct characteristics. More study is required, in particular in north-western and north-central Siberia, but in the small samples examined here, no evidence of such patterns has been found. Estimated correlations between studied plumage features (using Goodman & Kruskal's gamma) and between plumage features and hind claw length (using Pearson's R; then treating plumage feature scores as continuous variables) are generally weak (< +/-0.4) and/or not significant. For example, correlation between hind claw length and extent of supercilium in males is non-existent (r=-0.03) between Eastern Taimyr and Lower Kolyma and weakly positive (r=0.31) but not statistically significant (T-test; p=0.1) between Yamal/Ob river basin and Western Taimyr.

Field studies have not revealed any correspondence between scores for different plumage features and calls or songs within regions. Birds with a prominent supercilium have used the same calls and song types as dark-headed birds in the same locations.

Discussion

Observations in Arctic populations

The examined material paints a rather complex picture of variation across the Arctic regions, as summarised below and in figure 29. The main observations are: ***1*** average hind claw length increases between Komi and Nenets Autonomous Okrug (NAO) and Yamal/Ob river basin; ***2*** on average, first-winter plumage colouration is greyer in Komi and area between Yamal/Ob river basin and Taimyr compared with birds in northern Europe, and greyer still between Lower Indigirka and Chukotka and Alaska; ***3*** female plumage colouration gradually becomes more male-like on average between Arkhangelsk and Lower Yenisey and Taz; ***4*** on average, dark spotting on the upper breast becomes more prominent and the extent of white on the throat in males becomes more extensive between Taimyr and Lower Anabar; ***5*** the extent of a white supercilium in males varies in most parts of the Arctic but dark-headed birds dominate from Northern Scandinavia eastwards to Western Taimyr. The average extent of supercilium increases between Western Taimyr and Eastern Taimyr, and then again between Lower Kolyma and Chukotka, with birds with a prominent supercilium dominating in Chukotka and Alaska; ***6*** the single-note song type dominates in Northern Scandinavia eastwards to Western Taimyr. This song type is seemingly absent in Chukotka, Kamchatka and Alaska, where

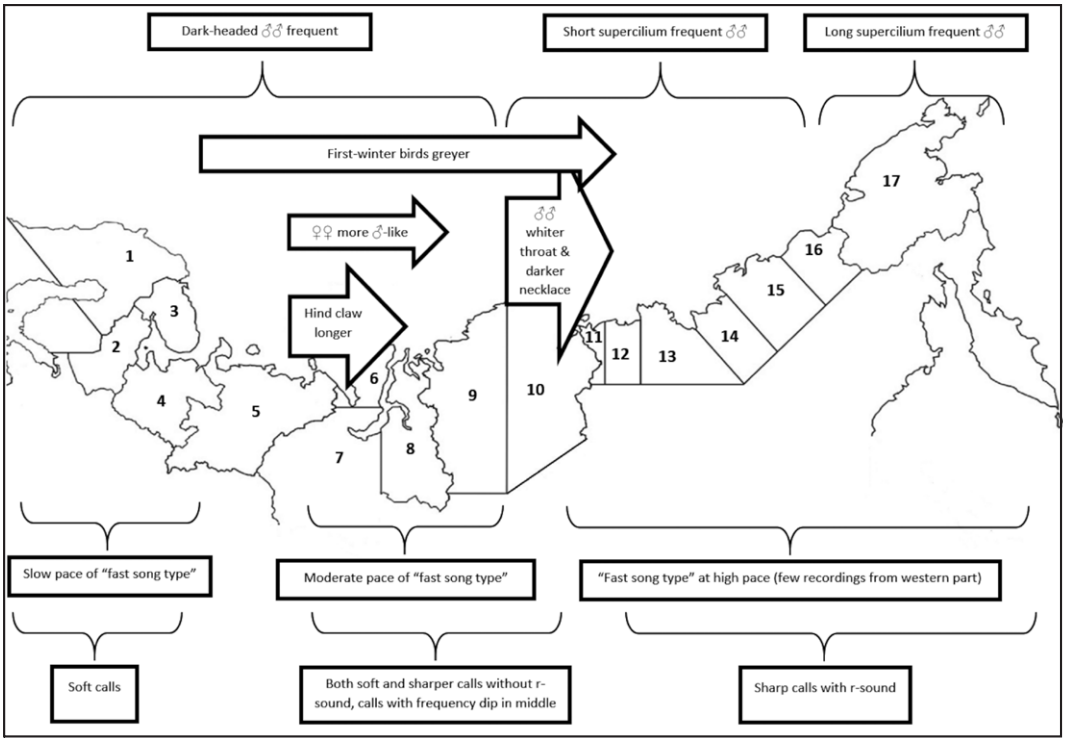

FIGURE 29 Approximate overview of distribution (brackets) and shifts (arrows) in examined features in yellow wagtail *Motacilla flava* sensu lato across the Arctic regions. Numbers refer to regions defined in figure 1. Further studies including larger samples and additional features are needed to understand geographical variation in more detail.

sampled birds only used the fast song type. The fast song type is regularly used in Northern Scandinavia as well but, here, the average number of notes per phrase is lower, the pace is slower and the voice is less ringing and lower pitched on average. Between the Ob river basin and Western Taimyr, the fast song type is intermediate between that given in Northern Scandinavia and in Chukotka, Kamchatka and Alaska. Between Eastern Taimyr and Lower Kolyma, only the fast song type has been documented but few recordings are available. Here, the song seems rather similar to that in Chukotka, Kamchatka and Alaska, although the average pace is slightly slower and average number of notes per phrase might be lower; ***7*** Scandinavian birds give mostly soft contact calls. From the Ob river basin and Yamal to Taimyr, sharper calls are given alongside soft ones but still without noticeable *r*-sound. East of Taimyr and in Alaska, birds give sharp calls with a conspicuous *r*-sound. Between Yamal/Ob river basin and Taimyr, a distinct call with a frequency dip midway is given alongside other call types.

Genetic research

The results can be viewed in light of existing genetic research on yellow wagtails. Several studies have identified a deep genetic divide between Western Yellow Wagtail and Eastern Yellow Wagtail based on mitochondrial DNA (mtDNA) (Ödeen & Alström 2001, Alström & Ödeen 2002, Voelker 2002, Ödeen & Björklund 2003, Pavlova et al 2003, Drovetski et al 2018, Harris et al 2018). Pavlova et al (2003) demonstrated that birds carrying a mtDNA haplotype typical of northern Eastern Yellow occur at least as far west as the Ob river basin (Labytnangi). Here, specimens carrying Western Yellow mtDNA have also been collected but their share is apparently lower: two out of 27 sampled by Drovetski et al (2018).

Based on analyses of large sets of genome wide data, Harris et al (2018) found a much less pronounced divergence between Western Yellow Wagtail and Eastern Yellow Wagtail. The data failed to distinguish between the phenotypically distinct taxa recognised in current taxonomy, conforming to a large extent with gradual isolation by

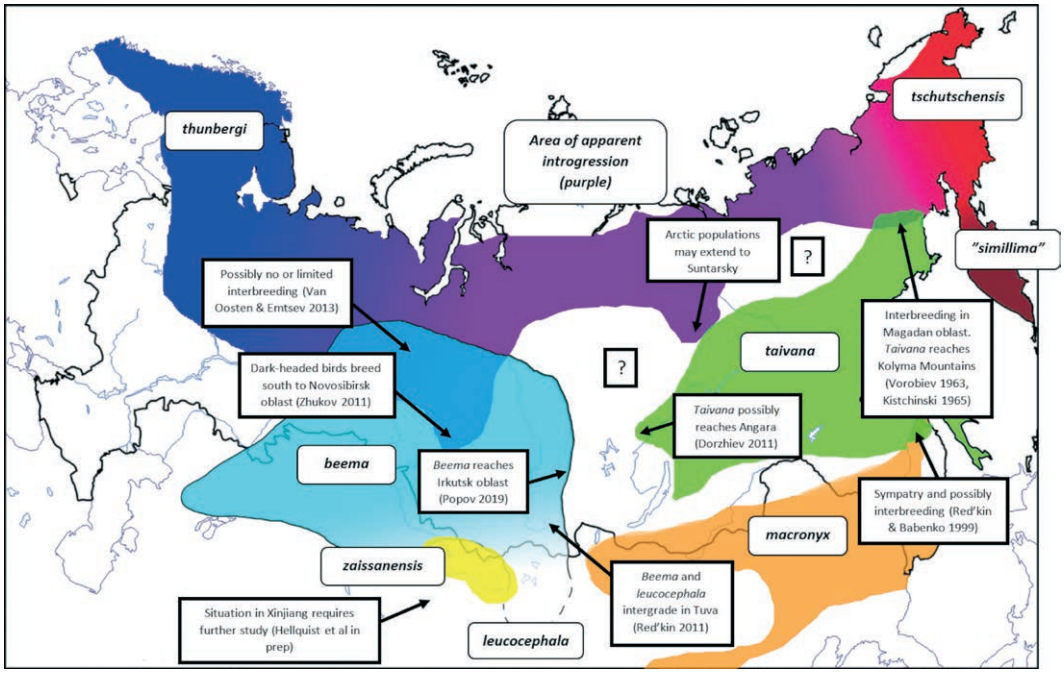

FIGURE 30 Approximate breeding distribution of studied northern and eastern populations of yellow wagtail *Motacilla flava* sensu lato based on reviewed material (cf table 1). Distributions of *flava*, *lutea* and *feldegg*, which also breed in western parts of area shown on map but have not been studied in detail here, are not shown, and neither is *tschutschensis* population in Alaska.

distance, although the authors identified two barriers with potentially restricted gene flow (Harris et al 2018; fig 4c, p 189): one separating populations breeding westwards from north-western Russia, Kazakhstan and western Mongolia from populations further east, and one separating northern Siberian and Alaskan birds from the south-eastern populations that comprise *macronyx* and *taivana*. The authors estimated roughly equal probabilities for sampled specimens from Labytnangi and Nyabrsk to belong to either Western Yellow or northern populations of Eastern Yellow, whereas specimens from Eastern Taimyr and eastwards (Lower Anabar, Lower Kolyma, Chukotka) were assigned to northern Eastern Yellow.

Introgression

The results of this study are consistent with a broad zone of differential introgression between Western Yellow Wagtail and Eastern Yellow Wagtail in the Russian Arctic, thus contrasting markedly with genetic studies showing a deep divide between the species based on mtDNA but seemingly less so with the SNP analysis in Harris et al (2018).

The shifts in examined plumage features and vocalisations seem to occur partially in separate geographic regions, and no indications of sympatry between populations showing distinct sets of features have been found. Sexual selection based on head pattern has been suggested as a mechanism behind rapid emergence of different male yellow wagtail phenotypes, despite limited genetic divergence (Ödeen & Björklund 2003). Still, the substantial share of males with intermediate head patterns across the Arctic regions suggests introgression in a zone of secondary contact between populations of dark-headed birds and birds with supercilium. Additional studies including larger samples are needed to evaluate whether the apparent increase over time in shares of males with supercilium between Karelia and Yenisey and Taz and the apparent increase in shares of dark-headed birds between Taimyr and Lower Kolyma are signs of ongoing diffusion of formerly distinct populations.

In the western part of the Arctic, it is conceivable that the head pattern is subject to influence from Arctic populations to the east, *flava* and *beema* populations to the south, or both. Southern

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492 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male intergrade *taivana x tschutschensis*, Magadan, Russia, 21 June 2008 *(Lars Petersson)*. Intergrades between these subspecies seem to occur regularly in Magadan oblast, while intergrades between *taivana* and *simillima* occur in southern Kamchatka (online photographs, own observations). **493** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *macronyx*, Bayannuur, Mongolia, 5 June 2018 *(Niklas Andersson)*. Compared with dark-headed Arctic birds, *macronyx* show cleaner yellow breast on average. **494** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *macronyx*, Bayannuur, Mongolia, 5 June 2018 *(Niklas Andersson)*. Example of bird with few white feathers above eye.

thunbergi populations breeding in, eg, central Sweden, southern Finland, the Baltic countries, Belarus and around Moscow and St Petersburg, Russia, where *flava* phenotypes also occur, have not been included in this study, but it is possible that influence from *flava* and *beema* reaches Arctic regions. This could explain the slightly higher average scores in the more southerly Karelia and Arkhangelsk regions compared with the Northern Scandinavia and Murmansk regions (figure 12). Further study is also needed to pursue the suggestion that based on different habitat preferences, *beema* and dark-headed birds occur sympatrically with no or limited interbreeding in the middle Ob river region (van Oosten & Emtsev 2013).

Introgression can change the phenotypic composition in zones of secondary contact over short periods of time, as demonstrated in Pine Bunting *Emberiza leucocephalos* and Yellowhammer *E citrinella* in southern Siberia (Panov et al 2003). Vocalisations can also evolve rapidly, in particular if they are partly learned and not only controlled genetically (eg, Ribot et al 2012), and might show no or only a weak association with genetic variation (MacDougall-Shackleton & MacDougall-Shackleton 2001, Soha et al 2004). This highlights potential difficulties in capturing recent dynamics based on old specimens. The area of apparent introgression in Arctic yellow wagtails is larger than that of hybridisation between Pine Bunting and Yellowhammer, which stretches from the Urals to lake Baikal, and much larger than known areas of introgression between Western Yellow Wagtail subspecies. A contributing factor might be that the density of Arctic populations seems rather low, with apparent concentrations of breeding pairs around settlements. Dispersal distances of yellow wagtails are among the largest measured in birds considering their body mass and diet (Sutherland et al 2000), which might enable populations to expand rapidly across large sparsely populated areas.

495 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Nizhny Kolymsk, Lower Kolyma, Russia, 12 June 1912 *(Jeremiah Trimble/MCZ)*. Holotype of *plexa* (MCZ 64033). Males with this appearance can be found along entire Arctic from Scandinavia to Alaska, USA. Combination of rather extensive white on chin, dusky markings on breast (not visible in this photograph) and weak supercilium is frequent between Lower Kolyma and Lower Anabar. **496** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Sharagolskaya village, Baikal area, Russia, 15 June 1913 *(Vladimir Loskot/ZIN)*. Holotype of *angarensis* (ZIN 125666/466-960).

Plexa problem

The results of this study are of relevance for the definition of the Eastern Yellow Wagtail subspecies *plexa*, which is clouded by uncertainty. According to the original description (Thayer & Bangs 1914), *plexa* shows a 'very thin, but well-marked' supercilium separating it from *thunbergi*, and also more white on the chin. Plate 495 depicts the type specimen, collected in Lower Kolyma. The range of *plexa* is unclear. The western limit has been variably placed at the Pechora river (Grant & Mackworth-Praed 1952), approximately along the Urals (Red'kin et al 2016), at the Yenisey river (Sushkin 1925, Dementiev & Gladkov 1954), at the Taz river (Vaurie 1959), 'at least east from 83-85°E' (Bot et al 2014) or at the Lena river (Brazil 2009). The eastern limit is often given as the Kolyma river but some authors describe a zone of intergradation between *plexa* and *tschutschensis* from Kolyma to Anadyr in Chukotka (Dementiev &

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497 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Sharagolskaya village, Baikal area, Russia, 15 June 1913 *(Vladimir Loskot/ZIN)*. Paratype of *angarensis* (ZIN 125667/466-960). **498** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *zaissanensis*, Kalawu Tekele lake, northern Xinjiang, China, 19 May 2011 *(Alexander Hellquist)* **499** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *zaissanensis*, Kalawu Tekele lake, northern Xinjiang, China, 19 May 2011 *(Alexander Hellquist)*. This bird gave soft disyllabic calls (sonagrams figure 27C-E). **500** Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male *zaissanensis*, Kalawu Tekele lake, northern Xinjiang, China, 19 May 2011 *(Peter Schmidt)*. Bird with less prominent supercilium.

Gladkov 1954, Kistchinski 1988, Portenko 1989) while Red'kin & Babenko (1999) argue that *tschutschensis* reaches Kolyma and that the intergradation with *plexa* takes place further west.

Based on the results of this study, it is not possible to separate the population breeding in Lower Kolyma region from *tschutschensis* breeding in Chukotka and Alaska with enough confidence to meet the often applied 75% rule for subspecific recognition (eg, Amadon 1949). The only significant identified difference is the larger share of birds with dark heads or only a short supercilium around Kolyma but such phenotypes occur in Chukotka as well (plate 490). Further studies of song variation might establish additional differences. Westwards, birds from Lower Kolyma are very similar to populations at least as far as Lower Olenyok. Compared with breeders further west, in Taimyr, there is a seemingly consistent difference in typical contact calls, along with small average differences in male plumage and possibly also pace of song.

If *plexa* is to be regarded as a separate taxon (ignoring the 75% rule vis-à-vis *tschutschensis*), a logical delimitation of the range based on features studied here would be Lower Kolyma in the east and Lower Olenyok or Lower Anabar in the west (depending on vocalisations of breeders in Lower

501 Yellow wagtail / gele kwikstaart *Motacilla flava* sensu lato, male, Gornozavadovsk, Sakhalin, Russia, 9 July 1993 *(John Klicka/UWBM)*. Specimen identified as intergrade between *taivana* and *macronyx* by Red'kin & Babenko (1999) but present author considers that it falls within variation of *taivana* (however, specimen not examined by author).

Anabar). However, by such standards, the populations in Taimyr and westwards to the Ob river basin and Yamal can be argued to show a comparable degree of differentiation, being possible to separate from populations further west based on longer average hind claw, brighter plumage colouration in females, generally slightly sharper calls and also a potentially distinct call type.

If future studies confirm ongoing changes in appearance and vocalisations in north-western and north-central Siberia due to introgression, it might be better to view birds breeding here as intergrades between *thunbergi* and *tschutschensis* rather than as a separate taxon. Whether the pattern of introgression is consistent with a continued division of Western Yellow Wagtail and Eastern Yellow Wagtail into separate species also requires further attention. In general, wide zones of intergradation given dispersal distance indicate lack of reproductive barriers (eg, Barton & Gale 1993). Ongoing studies of complete genomes in yellow wagtails (Per Alström pers comm) will likely shed more light on this issue in the near future.

Simillima and *macronyx*

The results of this study align with the accounts of *simillima* and *macronyx* in Alström & Mild (2003). *Simillima* differs from *tschutschensis* only slightly in terms of cleaner yellow underparts with less prominent necklace and on average less white on the throat. Kistchinski (1980) describes an intergradation zone in northern Kamchatka where birds become even more similar to *tschutschensis*. Because of the small differences, the validity of *simillima* can be questioned.

Macronyx (plate 493-494) is similar to dark-headed Arctic birds. Upon direct comparison of series of specimens, its cleaner yellow underparts are evident. Few examined Arctic birds were equally bright, especially east of Taimyr. None of the examined *macronyx* showed a prominent necklace (score 3 in figure 8), as opposed to 55% in Arctic birds between Lower Anabar and Lower Kolyma. Conversely, only 5% of birds between Lower Anabar and Lower Kolyma showed clean yellow underparts as in a majority of *macronyx*. *Macronyx* also differs on average in terms of blunter wing, longer emargination on the eighth primary (Alström & Mild 2003), and to some extent genetics (Drovetski et al 2018, Harris et al 2018). Typical calls and song separate *macronyx* from dark-headed Arctic birds from Taimyr and westwards. As indicated by Bot et al (2014), there might also be small average differences in calls between *macronyx* and Arctic birds east of Taimyr. However, additional studies based on large samples are needed to confirm this.

Zaissanensis

Zaissanensis is treated as synonymous with *tschutschensis* by some authorities, eg, AOU (Banks et al 2004) and IOC (following Alström & Mild 2003), while Red'kin (2000, 2001) groups it with Western Yellow Wagtail. It seems that it is geographically isolated from all Eastern Yellow Wagtail subspecies, as suggested by Johansen (1944) and also indicated in the map in Red'kin et al (2016). While the male head pattern in *zaissanensis* and *tschutschensis* is similar, *zaissanensis* differs in softer calls, western-type songs, shorter hind claw length

and duller female plumage, suggesting that it is a western form. It also shows a cleaner yellow breast on average in males than *tschutschensis*. It seems that *zaissanensis* and *beema* intergrade to some extent (skins in ZMUC). Still, the darker crown and ear coverts distinguish studied *zaissanensis* in the Kazakh and Chinese Altai mountains from typical *beema*.

The breeding range of *zaissanensis* is bordered in the north by a broad belt running through Novosibirsk oblast, the Altai Republic, Kemerovo oblast, southern Krasnoyarski Krai and Tuva Republic, where *beema* breeds and intergrades with *leucocephala* in the east from Tuva to north-western Mongolia (Cvetkov et al 2003, Red'kin 2011). In the studied material, no evidence of *tschutschensis*-like phenotypes breeding in this belt, or anywhere else close to the Altai, has been found. Given the relative distinctiveness of *zaissanensis*, and its apparent isolation from similar phenotypes, two alternative hypotheses regarding its taxonomic position can be considered: ***1*** *zaissanensis* is a valid Western Yellow Wagtail subspecies with a restricted range in the Altai; ***2*** *zaissanensis* represents a stable population of intergrades between other taxa, if so, possibly *feldegg* and *beema* that breed in close proximity just west and north of its range.

In support of the intergrade hypothesis, it can be noted that the plumage of *zaissanensis* is similar to that of '*dombrowski*' intergrades between *flava* and *feldegg* in south-eastern Europe, which in turn are similar to *tschutschensis* (as described in Alström & Mild 2003). Presumably, intergrades between *feldegg* and *beema* can also be similar to '*dombrowski*'. Intergradation between *feldegg* and *beema* in Trans-Caspia is mentioned by Stepanyan (1990) and Alström & Mild (2003). *Feldegg* has expanded eastwards in Central Asia as deserts have been turned into arable land (Ferlini 2016), which might increase potential for interbreeding with other taxa. Odd phenotypes including '*supercilliaris*', '*melanogrisea*' as well as grey-headed birds without a supercilium breed in Xinjiang just south of the range of *zaissanensis*. It is conceivable that all of these, as well as *zaissanensis*, represent an intergradation zone (although the grey-headed birds might better be regarded as a distinct separate subspecies; Hellquist et al in prep). The typical rasping call of *feldegg* was not noted in the small sample of studied *zaissanensis*. The vocal repertoire of *feldegg*, however, is broad and soft calls are frequent.

On the other hand, the appearance of *zaissanensis* males in the studied sample is rather consistent (plate 498-500), with variability in male plumage seemingly equivalent to that in other yellow wagtail subspecies. In addition, it seems that *zaissanensis* has a fairly well-defined distribution in the Altai where other phenotypes are absent or very rare, although further study is needed to confirm this.

Angarensis

The apparent isolation of *zaissanensis* from Eastern Yellow Wagtails is relevant also when discussing the status of *angarensis*, another taxon clouded by uncertainty. It was described by Sushkin (1925) based on two males collected by Sharagolskaya village south-east from lake Baikal on 15 June 1913, along with six more specimens from central Siberia. The holotype and the paratype collected in the same location are depicted in plate 496-497. Sushkin (1925) defined the range of *angarensis* as Transbaikalia, northern Baikal, the Tunguska river basins and the headwaters of the Khatanga river. Little convincing evidence that birds reminiscent of the two type specimens, or of *tschutschensis* in general, breed in this area has been found in the literature or in the examined material.

Taivana seems to be the only yellow wagtail breeding in east-central Siberia. To the west, it reaches areas north of lake Baikal and possibly the upper reaches of Angara (Dorzhiev 2011, Volkov 2016). Popov (2016) mentions '*tschutschensis*' as a rare passage migrant only in Prebaikalia (ie, regions just west of lake Baikal), and states that it is not breeding in the northern Irkutsk oblast along Lower Tunguska. Igor Fefelov (in litt) asserted that presently no yellow wagtails breed in southern Irkutsk oblast, while *beema* has recently been found breeding in the westernmost part of Irkutsk oblast by Chuna river (Popov 2019). In his account of birds in Yakutia, Vorobiev (1963) mentions *angarensis* only as a passage migrant in the eastern parts (it seems likely that he refers to *tschutschensis* phenotypes) while Ivanov (1935) states that *taivana* is the only breeding subspecies in the central part of Yakutia. In an account of the avifauna of the southern Baikal region, Mel'nikov (2017) asserted that *tschutschensis* is a rare passage migrant, that *taivana* is a sparse passage migrant, and that *macronyx* is accidental but has possibly bred occasionally in recent years. Rogacheva & Vakhrushev (1983) suggest that yellow wagtails are rare or absent as breeders in the taiga zone along middle Yenisey river, north of the *beema* populations breeding around Krasnoyarsk, while stating that they become common northwards at least from the Baklanikha river tributary. Here, breeding birds should be connected with the Arctic populations

included in this study. Romanov (2015) states that yellow wagtails are locally common breeders on the Putorana plateau south of the Taimyr peninsula, ie, just west of the Khatanga river headwaters. Only one specimen from the Putorana plateau, a female, has been examined. Again, this population should be connected with those sampled from Taimyr. Dementiev & Gladkov (1954) assert that *angarensis* is a 'highly dubious subspecies' but they restate the range given by Sushkin (1925) and add that it might extend eastwards almost to Verkhoyansk and along the Yana river. The examined specimens from the northern parts of these regions are not distinct from other Arctic breeders between Anabar and Kolyma.

Apart from the examined type specimens, the only indication of birds matching the description of *angarensis* breeding well south of the Arctic is a male collected on 2 July 1965 in the Suntarsky district in south-western Yakutia (ZMMU 103702). It is similar to *tschutschensis*, with a prominent supercilium. It is also similar to birds with a prominent supercilium collected in the Lower Anabar region, almost straight north from Suntarsky district (there are also dark-headed birds breeding in the Lower Anabar, as evident among skins at ZMMU and also described by Gladkov & Zalataev 1964/2014). It is conceivable that the specimen from the Suntarsky district represents a current or former population of central Siberian birds with a white supercilium, or a southern extension of Arctic populations, but it could also be a non-breeding bird south of its normal range.

The same uncertainty regarding breeding status applies to the *angarensis* holotype and paratype. Although they were collected during the period of breeding around lake Baikal, it seems that the spring passage of *tschutschensis* phenotypes through this area extends into June, with migrating birds noted along the north-western shores on 5 June 2005 by Magnus Hellström (www.club300.se/Files/TravelReports/Siberia2005_MH.pdf). As evident in plate 496-497, the plumage of the *angarensis* paratype matches *tschutschensis* well, whereas the holotype has a dark crown and ear-coverts and a long supercilium that is partly yellow behind the eye. In this regard, it is slightly atypical. *Tschutschensis* occasionally shows yellow hues in the supercilium and the darkness of the crown varies, just as in other Arctic populations. Therefore, the *angarensis* holotype probably falls within variation of *tschutschensis* and other Arctic birds with a supercilium but an intergrade might also be considered given that the specimen was collected in between the main ranges of *taivana* and *macronyx*. Very few intergrades between these two taxa have been described in literature, and no convincing case has been found during this study. Photographs of a specimen identified by Red'kin & Babenko (1999) as an intergrade between *taivana* and *macronyx* (UWBM 46975) have been examined (plate 501). In my view, it falls within the variation of *taivana*.

Another possibility is that the *angarensis* type specimen represents an intergrade between *taivana* and either *tschutschensis* or *simillima*, which seem to occur regularly in Magadan oblast and southern Kamchatka (eg, plate 492). Pending genetic analysis that clarifies the identity of the holotype, the best option is probably to consider *angarensis* a likely northern passage migrant rather than a valid separate taxon, as indeed suggested by Meinertzhagen (1954). It can be noted that Red'kin et al (2016) omitted it from their account and leave a large part of its range empty in their distribution map.

Conclusions

To summarise the main findings of this study, the variation in sampled birds across Arctic regions suggests introgression between *thunbergi* and *tschutschensis* between Lower Ob and Lower Kolyma, challenging the division into two separate yellow wagtail species. Overlap between birds from different regions makes it impossible to identify geographic origins of out of range individuals based on measurements and plumage features examined here. However, average differences may provide clues, and when combined with recordings of series of typical contact calls and song, it is possible to assign birds with reasonable certainty to three areas: ***1*** Scandinavia and north-western Russia: soft calls that are often slightly disyllabic; song either single note type or slow variants of fast type; ***2*** The area between Yamal/Ob river basin and Taimyr: sharper calls without *r*-sound and calls with prominent frequency dip midway; song either single-note type or fast type at moderate pace; ***3*** The area east of Taimyr and in Alaska: sharp Citrine Wagtail-like calls with *r*-sound; song most likely only a fast type at high pace (more study of song needed in area between Eastern Taimyr and Lower Kolyma). Based on examined features, it is not possible to separate birds breeding east of Taimyr to Lower Kolyma, ie, within the alleged range of *plexa*, from *tschutschensis* with enough confidence to meet the 75% rule for subspecific recognition, although males without a supercilium are regular in Lower Kolyma and westwards while being rare in *tschutschensis*.

For the more southern taxa, the findings corroborate earlier studies showing only slight average differences between *simillima* and *tschutschensis*, and more pronounced and consistent average differences in plumage between *macronyx* and Arctic dark-headed birds. No convincing evidence of the existence of the alleged taxon *angarensis* has been found. Finally, the results suggest that *zaissanensis* is a fairly distinct form of Western Yellow Wagtail. Its consistent plumage and separate breeding range in the Altai mountains suggest that it is a valid subspecies (Yaroslav Red'kin in litt), although further study is needed to firmly rule out the possibility of an intergrade population.

From a European field identification perspective, the findings confirm that recordings of calls are essential when dealing with suspected vagrant eastern yellow wagtails. Actually, in Arctic populations, calls seem to provide a more precise indication of geographic origin than the mtDNA haplotypes upon which publication of Eastern Yellow Wagtails records in Europe has relied heavily so far. As long as the status of *plexa* is unresolved, assignment of north-eastern birds to a specific taxon will however remain problematic.

Acknowledgements

I am indebted to a large number of people who have helped me in various ways during the preparations of this paper: Janne Aalto, Per Alström, Niklas Andersson, Göran Bength, Lotta Berg, Sharon Birks, Giovanni Boano, Peter Boesman, Jan Bolding Kristensen, Yuri Bykov, José Luis Copete, Magnus Corell, Laurent Demongin, Kevin Epperly, Igor Fadeev, Rob Faucett, Igor Fefelov, Thijs Fijen, Jon Fjeldså, Michaela Forthuber, Fredrik Friberg, Dirk van Gansberghe, Igor Gavrilov, Mikhail Gennadevich, Sulli Gibson, Petter Haldén, Louis A Hansen, Magnus Hellström, Martti Hildén, Ulrich Joger, Ulf Johansson, Lars Jonsson, John Klicka, Sergey Kochanov, Niels Krabbe, Dennis Kraft, Hans Larsson, Vladimir Loskot, Łukasz Ławicki, Björn Malmhagen, Ola Marklund, Bob Mcguire, Sergey Michailovich, Benny Modig, Gleb Nakul, Nikolay Neufeld, Stein Ø Nilsen, Peter Nilsson (NRM), Peter Nilsson (Piteå), Thomas Noah, Herman van Oosten, Lars Petersson, Daniel Petterson, Jelmer Poelstra, Robert Prŷs-Jones, Edmunds Racinskis, Yaroslav Red'kin, Chris van Rijswijk, Magnus Robb, Peter Schmidt, Bill Schmoker, Manuel Schweizer, Andrey Semenov, Elena Shutova, Sergey Sleptsov, Håkan Sundin, Piotr Szczypinski, Dmitryi Tananenko, Pavel Tomkovich, Till Töpfer, Jeremiah Trimble, Ilya Ukolov, Peter de Vries, Mats Waern, Chris Wood and Christoph Zöckler.

Samenvatting

HERKENNING EN TAXONOMIE VAN NOORDELIJKE EN OOSTELIJKE GELE KWIKSTAARTEN – NIEUWE PUZZELSTUKJES Dit artikel presenteert gegevens over de variatie in morfologie, kleed en geluiden van noordelijke en oostelijke gele kwikstaarten *Motacilla flava* sensu lato. Om praktische redenen wordt hier de taxonomische indeling gevolgd conform *Handbook of the birds of the World* (del Hoyo & Collar 2016; westelijke *flava*-soortgroep en oostelijke *tschutschensis*-soortgroep), met focus op de Arctische ondersoorten *M f thunbergi*, *M t plexa* en *M t tschutschensis* en de meer zuidelijke *M t angarensis*, *M t simillima* en *M t macronyx*. Tevens wordt de vorm *zaissanensis* besproken.

De variatie in onderzochte vogels uit de Arctische regio's, van Europa oostwaarts door Rusland tot de Beringstraat en Alaska, VS, suggereert introgressie tussen *thunbergi* en *tschutschensis* tussen de benedenlopen van de Ob en de Kolyma, waarmee de indeling als twee aparte soorten (Gele Kwikstaart *M flava* sensu stricto en Oostelijke Gele Kwikstaart *M tschutschensis*) ter discussie komt te staan. De overlap tussen vogels van verschillende Arctische regio's maakt het onmogelijk om de geografische herkomst te bepalen van afgedwaalde individuele vogels op basis van maten en kleedkenmerken. Echter, gemiddelde verschillen kunnen aanwijzingen bieden en in combinatie met opnamen van series typische contactroepen en zang is het mogelijk om individuen met een redelijke mate van zekerheid te koppelen aan drie gebieden: ***1*** Scandinavië en waarschijnlijk Noordwest-Rusland: zachte roepen die vaak iets tweelettergrepig zijn, en zang van het eentonige type of een langzaam meertonig type; ***2*** het gebied tussen het Yamal/Ob-bekken en Taimyr: scherpere roepen zonder *r*-klank en roepen met een opvallende dip in frequentie halverwege, en zang van het eentonige type of een meertonig type met gematigd tempo; en ***3*** het gebied ten oosten van Taimyr en in Alaska: scherpe Citroenkwikstaart *M citreola*-achtige roepen met *r*-klank, en zang van zeer waarschijnlijk alleen een meertonig type in hoog tempo. Op basis van de onderzochte kenmerken is het niet mogelijk om broedvogels ten oosten van Taimyr tot de benedenloop van de Kolyma (ie, binnen het veronderstelde gebied van *plexa*) met voldoende zekerheid (de 75%-regel voor erkenning als aparte ondersoort) te onderscheiden van *tschutschensis*, hoewel mannetjes zonder wenkbrauwstreep regelmatig voorkomen in het gebied van de benedenloop van de Kolyma en ten westen daarvan, terwijl dat kenmerk zeer zeldzaam is in *tschutschensis*.

Voor de meer zuidelijke taxa bevestigen de resultaten eerdere studies die slechts geringe gemiddelde verschillen toonden tussen *simillima* and *tschutschensis*, en de meer uitgesproken en consistente kleedverschillen tussen *macronyx* en Arctische donkerkoppige vogels. Er is geen overtuigend bewijs gevonden voor de validiteit van het veronderstelde taxon *angarensis*. Ten slotte suggereren de resultaten dat *zaissanensis* een vrij duidelijke vorm is van de westelijke groep. Het consistente verenkleed en gescheiden broedgebied in het Altai-gebergte suggereren dat het een valide ondersoort is, hoewel verder onderzoek nodig is om de mogelijkheid van een overgangspopulatie uit te kunnen sluiten.

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APPENDIX 1 Overview of studied yellow wagtails *Motacilla flava* sensu lato in breeding grounds

Geographic region/taxon (numbers refer to regions in figure 1)	**Field studies by author**	**Number of examined individuals in field photographs**	**Number of examined museum specimens**	**Number of singing individuals in examined recordings**	**Number of calling birds in examined recordings**
1 Northern Scandinavia	X	152	196	26	44
2 Karelia		3	6	1	2
3 Murmansk		15	15	0	0
4 Arkhangelsk		2	18	0	0
5 Komi & NAO		16	24	0	2
6 Yamal		20	10	0	11
7 Ob river basin	X	21	50	16	44
8 Lower Yenisey and Taz	X	66	24	1	23
9 Western Taimyr	X	18	6	12	24
10 Eastern Taimyr	X	26	13	1	19
11 Lower Anabar		0	15	0	0
12 Lower Olenyok	X	10	0	2	9
13 Lower Lena	X	5	10	2	5
14 Lower Yana		0	27	0	1
15 Lower Indigirka		6	21	2	3
16 Lower Kolyma		10	42	0	0
17 Chukotka	X	10	69	1	3
18 Alaska	X	53	10	10	28
19 Kamchatka (*simillima*)	X	27	25	2	8
beema	X	28	17	9	10
zaissanensis	X	23	34	3	5
macronyx		8	27	9	9