Putative Segregation of Two Yellow Wagtail Taxa by Breeding Habitat in Western Siberia: Possible Implications for Motacilla flava Taxonomy

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Putative segregation of two Yellow Wagtail taxa by breeding habitat in Western Siberia: possible implications for *Motacilla flava* taxonomy

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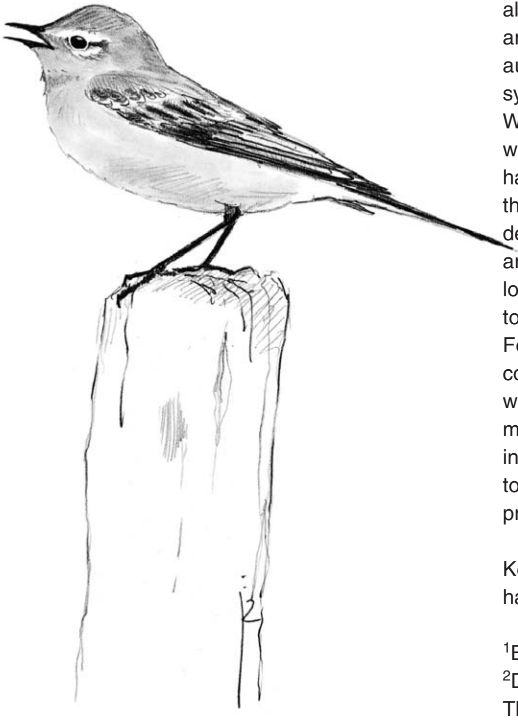

The Yellow Wagtail *Motacilla flava* consists of about 18 taxa whose taxonomic relationships are unclear. Some authors elevate 11 taxa to species based on often characteristic nuptial plumages of males, whereas others recognize two species based on molecular data. Hybridization is a regular event but with intriguingly varying intensity between different taxa. In spite of breeding generally in damp fields, their breeding habitat is actually rather diverse, which offers an opportunity for ecological segregation by breeding habitat. Indeed, some authors describe habitat differences between taxa but others do not. Two sympatrically occurring taxa are *thunbergi* and *beema* in European Russia and Western Siberia. In this study we describe their breeding habitat and determine whether this differs between taxa. We aimed to determine whether breeding habitat could be an ecological factor for sub-specific segregation in this part of their breeding range. We found strong indications for segregated breeding, despite the rather limited dataset: *thunbergi* occurred in bogs as a breeding bird and *beema* was dominantly found breeding in floodplain meadows. On one location bog and floodplain were separated by only 1.5–2 km of forest, yet here too only *thunbergi* occurred on the bog and *beema* on floodplain meadows. Following recent molecular taxonomic findings our *thunbergi* might very well concern *plexa*, belonging to the eastern species. As *beema* is assigned to the western species, the observed spatial segregation between *plexa* and *beema* may be representative of habitat separation of the western and eastern species in areas where they occur sympatrically. Large scale segregated breeding due to different habitat preferences could have consequences for taxonomic interpretations within the *M. flava* complex.

Key words: Yellow Wagtail, taxonomy, *Motacilla flava*, *thunbergi*, *beema*, *plexa*, habitat requirements, ecological segregation, Siberia, Russia

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Radiation in Yellow Wagtails *Motacilla flava* has resulted in a species-swarm of about 18 taxa which are distinguishable by the often characteristic summer nuptial plumages of adult males (Alström & Mild 2003). Yet, in spite of distinctive plumage differences, the taxonomic status of all taxa is as yet far from resolved. Some authors recognize only *M. flava* as a polymorphous species (e.g. Glutz von Blotzheim & Bauer 1985, Tyler 2004), whereas others elevate 11 taxa to species status based on differences in morphology of adult males (Sibley & Monroe 1990, Sangster *et al.* 1999).

Recent molecular studies indicate a likely polyphyletic origin of *M. flava*. Based on sequences of mitochondrial DNA Voelker (2002) and Pavlova *et al.* (2003) grouped all taxa into three clades which, as they state, should be considered species. Ödeen & Björklund's (2003) study on mitochondrial and nuclear DNA, however, merged the two eastern clades but

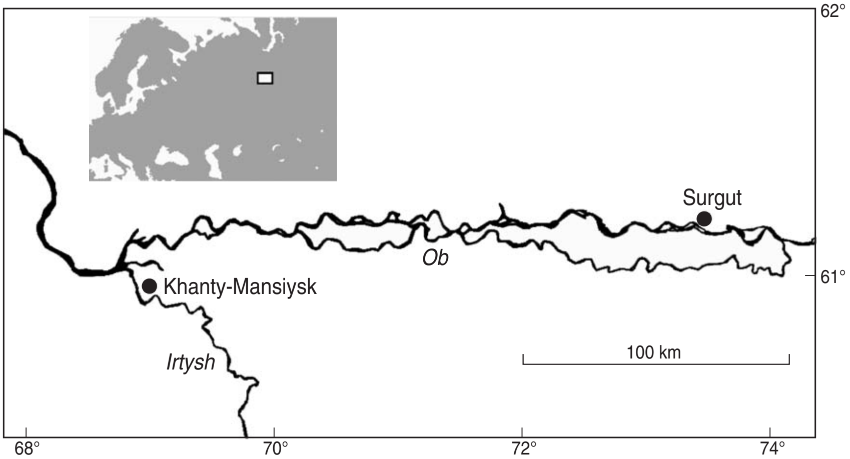

Figure 1. Map showing the study area along rivers Ob and Irtysh, with towns Khanty-Mansiysk and Surgut, Russia.

supported the western clade of Voelker (2002) and Pavlova *et al.* (2003), effectively implying two separate species within the *M. flava* complex. Obviously, Yellow Wagtail taxonomy is in a state of flux and as Tyler (2004, p.695) states "a great deal of additional research is required, both in the field and in the laboratory, before the relationships (…) of the taxa are understood."

If all western taxa belong to one monophyletic species (Voelker 2002, Ödeen & Björklund 2003, Pavlova *et al.* 2003), hybridization should occur between sympatric taxa. Though hybridization is often reported and hybridization zones exist (Glutz von Blotzheim & Bauer 1985), assigning individuals to hybrid forms is not always straightforward due to phenotypic variability within populations of a given taxon. In populations of dark-headed birds, for instance, individuals with clear eyebrows are reported though no neighbouring taxon with eyebrows occurs, which makes hybridization as a cause unlikely (Glutz von Blotzheim & Bauer 1985). Therefore, the regularity with which hybridization occurs might be difficult to ascertain. Some taxa (*iberiae*, *thunbergi*, *feldegg*, *beema* and *lutea*) are not reported to interbreed extensively when occurring in sympatry (Glutz von Blotzheim & Bauer 1985). For instance, the South European *iberiae* and cinereocapilla are geographically each other's neighbours but not known to interbreed and their wintering areas are widely separated as well (Alström & Mild 2003). Additionally, *feldegg* interbreeds only to a limited extent with *beema* with which it does occur in sympatry (Glutz von Blotzheim & Bauer 1985).

Since some taxa within the western species (Voelker 2002, Ödeen & Björklund 2003, Pavlova *et al.* 2003) are less prone to hybridization than others, there seems to be incongruence between contemporary molecular insights and what is actually happening on the breeding grounds. General as their habitat preferences may seem, Tyler (2004) specifies those habitats as rather diverse "from damp meadows, marshes (…), bogs to damp steppe and grassy tundra." These subtle yet distinct differences in vegetation and structure could provide an opportunity for segregation by breeding habitat requirements. Indeed, some authors describe varying habitat preferences between neighbouring taxa (Dement'ev & Gladkov 1954, Bakhtadze & Kazakov 1985, Glutz von Blotzheim & Bauer 1985, Boyko 1998a, 1998b, Alström & Mild 2003). It is clear that besides molecular studies, more field studies are needed to assist in clarifying taxonomy and habitat requirements of different *M. flava* taxa.

Two allegedly interbreeding taxa are *thunbergi* and *beema* (Alström & Mild 2003), which geographically occur in little studied sympatry, along the borders of their summer ranges in European Russia and Western Siberia (Dement'ev & Gladkov 1954). By visiting their West-Siberian environs of sympatry we determined whether both taxa share their breeding habitat. We aimed to determine whether breeding habitat could be an ecological factor for sub-specific segregation in this part of the breeding range of *thunbergi* and *beema*.

Methods

Between 2002 and 2012 we made opportunistic observations during ornithological expeditions in the Khanty-Mansi Autonomous Okrug (Western Siberia, Russia), where we visited extensive *Sphagnum* bogs (n = 12 locations; Appendix 1) and the vast floodplains of the rivers Irtysh, Ob and tributaries (n = 7 locations; Appendix 1). All locations were in an area of approximately 300 km by 200 km, roughly between towns Khanty Mansyisk and Surgut (Figure 1). This area is

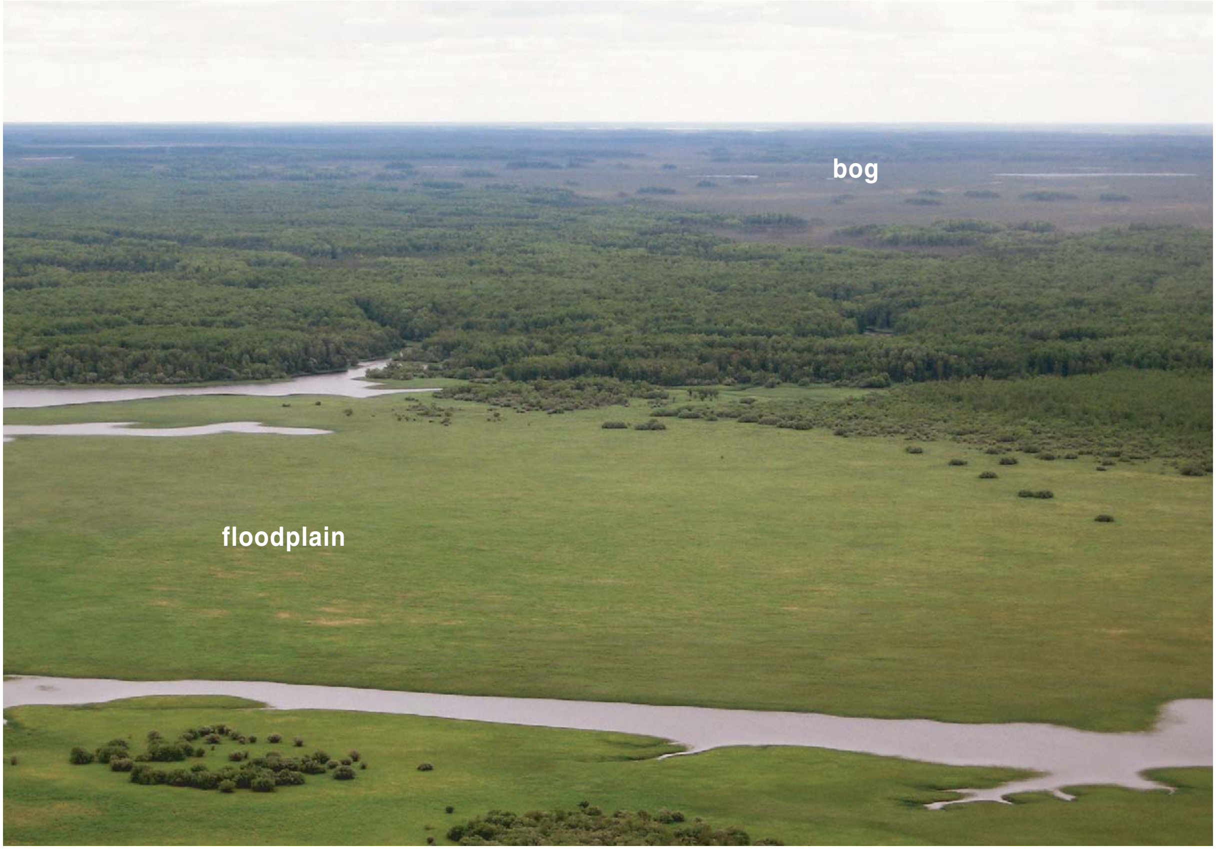

Figure 2. Floodplain and bog are separated by 1.5–2 km of forest near Mukhrino Field Station, where *thunbergi* and *beema* occur on either side of the forest ecotone (photo Rick Ruijs).

allocated in a broad zone of sympatry of both taxa, which in Western Siberia is roughly between 55°–60°N (Red'kin 2001, Ryabitsev 2008). Since *thunbergi* and *beema* are long-distance migrants (Glutz von Blotzheim & Bauer 1985) we are keen to distinguish occasional migrants from breeding birds. Migrants can turn up in any damp habitat, a potential pitfall when studying the birds' breeding habitat. To minimize confusion we decided to only use observations of feeding or strongly alarming parents, indicating the presence of (fledged) juveniles. Upon finding birds meeting our criteria we established their sub-specific identity. Fortunately, males of both taxa are easy to separate in the field: *thunbergi* males have a distinctive all dark head and a yellow throat, whereas *beema* males have a light, blue-grey head, a strong supercilium and a white throat (Alström & Mild 2003). There is controversy over the taxonomic status of dark-headed birds east of the Ural Mountains. These birds are widely recognized as belonging to the taxon *plexa* (Tyler 2004) but the validity of the taxon has been a subject of debate. Alström & Mild (2003) merged *plexa* with *thunbergi* since *plexa* specimens appeared indistinguishable from *thunbergi*, based on plumage and morphological characteristics. Therefore, and because *thunbergi* takes nomenclatural precedence over *plexa* (Tyler 2004), we choose to assign our dark-headed birds to *thunbergi*, though we are aware that they might refer to *plexa* since our site is close to collecting sites of *plexa* (Pavlova *et al.* (2003).

Females are much more difficult to separate, and to avoid faulty identification we focussed on adult males only. Next, we described vegetation composition of breeding habitat and carefully investigated the site for breeding birds.

Results and discussion

We found indications of differential habitat preferences in *thunbergi* (n = 12 locations, minimum of n = 97 birds; Appendix 1) and *beema* (n = 7 locations, minimum of n = 31 birds; Appendix 1). *Thunbergi* was only encountered as a breeding bird on *Sphagnum* bogs where we never saw breeding *beema*. The latter occurred as a breeding bird on floodplains of the river Irtysh and here *beema* was the predominant taxon breeding, despite careful searching.

As one would expect, floodplains and bogs differed tremendously in vegetation composition. *Sphagnum* bogs consisted of a mesh of ridges and hollows. On ridges dwarfshrubs *Ledum palustre*, *Betula nana* and *Rubus chamaemorus* grew within lush moss vegetation of *Sphagnum*, *Dicranum* and *Polytrichum*. The occasional oppressed *Pinus silvestris* grew as the only tree species on the breeding grounds of *thunbergi*. Lichens were only scantly encountered, and rarely one encountered *Eriophorum* and *Carex* sedges. In the moister hollows *Carex*, *Eriophorum*, *Menyanthes trifoliata* (and rarely *Comarum palustre*) grew. Moss cover consisted of *Sphagnum*, *Dicranum* and *Polytrichum*.

In contrast, the open, grassy floodplains were dominated by *Poaceae* (*Agrostis gigantea*, *Calamagrostis purpurea* and *Phalaroides arundinacea*), *Carex* spp. (*C. aquatilis*, *C. acuta*, *C. nigra* and *C. gracilis*) and occasional *Salix* trees.

Our observations are in concordance with Dement'ev & Gladkov (1954), who found that *thunbergi* generally occurs in peat bogs and *beema* on meadows and river valleys. Additionally, Boyko (1998a, 1998b) writes that "*thunbergi* generally [inhabits] *Sphagnum* bogs, and *beema* [is] mostly found in meadows, lowland bogs and near human habitation" in the Konda river lowlands (roughly at 60°42.2'N, 69°40.1'E, adjacent to the western borders of our study area). Given that *flava* and *beema* are closely related (Dement'ev & Gladkov 1954, Alström & Mild 2003), it is of interest to note that these results match a study in central Sweden, where *thunbergi* also breeds on bogs and *flava* in the adjacent meadows (Bylin 1974 in Glutz von Blotzheim & Bauer 1985).

In spite of our limited sample-size, segregation by strongly differing habitats appeared rather remarkable. As an example, near Shukhrino Field Station (60°53.2'N, 68°41.4'E), floodplain meadows and *Sphagnum*-bogs were separated by only 1.5–2 km of forest but here too, solely *thunbergi* occurred on the bogs and *beema* on the floodplains (Figure 2). However, in 2011 we observed individuals of both taxa along the lower reaches of the river Vynga (right tributary of the river Ob) in floodplain sedge meadows. Birds of both taxa were observed either alarming or feeding nestlings, indicating that both were breeding locally. The rarity of this observation is corroborated by remarks of Boyko (1998a), who states that "mixed pairs of both subspecies are not regular anywhere, though occasionally *beema* nests near *thunbergi* on *Sphagnum* bogs both in the Konda and Surgut regions." Alström & Mild (2003) however, report *thunbergi* and *beema* to intergrade in the northern Kirgiz steppes, but they do not provide details on the observed frequency of hybridization, or breeding habitat.

We conclude tentatively that *thunbergi* and *beema* appear to be largely segregated by breeding habitat in the area of study and this conclusion is corroborated by results of studies in other areas (Dement'ev & Gladkov 1954, Glutz von Blotzheim & Bauer 1985, Boyko 1998a, 1998b). However, given the still rather limited dataset and size of study area it remains to be seen whether this ecological segregation reflects the general situation along the vast area of sympatry of *thunbergi* and *beema*. If so, taxonomic conclusions based on breeding ecology are perhaps inconsistent with recent molecular findings (Voelker 2002, Ödeen & Björklund 2003, Pavlova *et al.* 2003).

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Samenvatting

Gele Kwikstaarten *Motacilla flava* vormen een taxonomisch onduidelijke soortenzwerm met circa 18 taxa. Sommige auteurs onderscheiden 11 soorten op grond van het vaak kenmerkende verenkleed van adulte mannetjes, maar andere auteurs erkennen slechts twee soorten gebaseerd op moleculaire inzichten. Het is duidelijk dat het laatste woord over de taxonomische indeling van Gele Kwikstaarten nog niet is gezegd. Hybridisatie tussen taxa treedt op, maar niet altijd even regelmatig en bij een aantal taxa minder dan bij andere taxa. Hoewel de soort broedt in vochtige graslanden lijkt er ruimte te zijn voor eventuele ecologische scheiding op grond van verschillen in het broedhabitat. Enkele auteurs beschrijven inderdaad habitatverschillen tussen verschillende taxa, maar anderen vinden geen verschillen. Twee taxa die naast elkaar voorkomen, zijn *thunbergi* en *beema* in Europees Rusland en West-Siberië. In de onderhavige studie onderzochten we of beide taxa in hetzelfde broedhabitat voorkomen en beschreven dit broedhabitat. Doel was te achterhalen of er sprake kan zijn van ecologische segregatie tussen deze taxa in het onderzoeksgebied. Ondanks het geringe aantal waarnemingen zijn er sterke indicaties voor een gescheiden voorkomen: *thunbergi* hebben we vrijwel alleen broedend aangetroffen in hoogveen, *beema* alleen in overstromingsvlaktes. Op één locatie waren de overstromingsvlakte en het hoogveen 1,5–2 km van elkaar gescheiden door bos, maar ook hier kwam *thunbergi* alleen in het hoogveen voor en *beema* alleen in de overstromingsvlakte. Zoals verwacht verschilden de hoogvenen en overstromingsvlaktes sterk in vegetatiesamenstelling. Op slechts één locatie vonden we *thunbergi* and *beema* naast elkaar: in een zeggenmoeras aan de Vynga-rivier. Op grond van recent moleculair-taxonomisch onderzoek lijkt *thunbergi* uit het onderhavige studiegebied op het taxon *plexa* betrekking te hebben. Dit taxon wordt toegewezen aan de 'Oostelijke Gele Kwikstaart'. Omdat *beema* bij de 'Westelijke Gele Kwikstaart' wordt ingedeeld, lijken deze twee (moleculaire) soorten van elkaar gescheiden door verschillen in broedhabitat in het betrekkelijk kleine studiegebied waar beide soorten sympatrisch voorkomen. Wanneer interspecifieke verschillen in broedhabitat bevestigd worden op een groter geografische schaal, kan dit consequenties hebben voor taxonomische indeling binnen het *M. flava* complex.

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Appendix 1. Locations, coordinates, dates and habitat of all *beema* and *thunbergi* observations in this study. Habitat types: FP-T = Floodplain bog with willow trees, FP-S = Floodplain sedge meadow, FP-G = Grassy floodplain, M = Grassy meadow, SPH = Sphagnum bog with ridges and hollows.

Taxon and site	Coordinates	Date	Habitat
Motacilla flava beema			
Near Saygatina, the valley of middle watercourse of the river Ob	61°15.6'N, 72°53.7'E	2–7–2008	M
Tren'ka, the valley of middle watercourse of the river Ob	61°13.0'N, 69°03.8'E	9–7–2004	M
The outskirts of Surgut, the valley of middle watercourse of the river Ob	61°14.8'N, 73°21.8'E	5–6–2009	FP-T
Near Shukrino Research Station	60°56.3'N, 68°42.3'E	15–6–2009	FP-G
River Irtysh, south of Khanty-Mansyisk	60°59.1'N, 68°57.2'E	25–6–2009	FP-G
Village of Shapsha	61°05.3'N, 69°27.6'E	14–6–2009	FP-G
Lower reaches of the river Vynga (right tributary of the Ob river)	61°20.0'N, 72°31.4'E	20–30–06–2011	FP-S
Motacilla flava thunbergi			
Tagrinskoe deposit, the basin of middle watercourse of the river Mohtik'yaun, near Raduzhnyy	62°16.5'N, 78°11.5'E	13–6–2004	SPH
Basin of middle watercourse of the river Mohtik'yaun, near Raduzhnyy	62°09.1'N, 77°54.5'E	17–6–2004	SPH
Near Lyantor, the basin of lower watercourse of the river Pim	61°35.8'N, 72°11.3'E	first half of June 2005	SPH
Saninskoe deposit (near Lake Antoplor), near Lyantor	61°52.0'N, 71°21.5'E	13–6–2005	SPH
	61°51.8'N, 71°21.3'E 61°51.1'N, 71°21.9'E	28–6–2005	SPH
Nazargaleevskoe deposit (near Lake Vilinglor), environs of Lyantor	61°44.6'N, 71°20.7'E	20–6–2005	SPH
	61°44.5'N, 71°21.6'E 61°44.5'N, 71°21.8'E 61°45.5'N, 71°21.7'E	18–6–2006	SPH
Russkinskoe deposit, the basin of lower watercourse of the river Muyunloryaun, near Russkinskaya	62°04.6'N, 73°28.1'E	29–5–2006	SPH
Lake Pil'tlor area, basin of lower watercourse of the river Sukur'yaun, near Russkinskaya	62°19.4'N, 73°03.7'E	4–6–2006	SPH
	62°19.4'N, 73°03.4'E 62°20.0'N, 73°01.2'E	6–6–2006	SPH
Konitlorskoe deposit, the basin of lower watercourse of the river Sukur'yaun, near Russkinskaya	62°22.1'N, 72°52.0'E 62°23.8'N, 72°52.4'E	6–6–2006	SPH
Luk'yavinskoe deposit, the Lake Kutlop'yaunlor area (near the river Lyuk'yagun), near Nizhnesortymskiy	62°56.2'N, 72°18.1'E 62°55.0'N, 72°18.6'E	24–6–2006	SPH
	62°56.5'N, 72°15.6'E	29–6–2006	SPH
Mur'yaunskoe (Tyanskoe) deposit, Lake Nankankillor area, near Nizhnesortymskiy	62°46.1'N, 72°09.7'E	03–10–07–2006	SPH
Near Shukrino Research Station	60°53.2'N, 68°42.1'E	16–6–2009	SPH
Lower reaches of the river Vynga (right tributary of the Ob river)	61°20.0'N, 72°31.4'E	20–30–06–2011	FP-S