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Migration of North Asian Passerines

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Abstract. The East Asian-Australasian bird migration system is one of the most species-rich migration systems, nevertheless, we have very little information on the migration of the species that use the Asian-Australasian Flyway. Most knowledge is available about waterfowls (cranes, ducks). However, very little is known about songbirds, mainly due to the lack of large-scale, long-term ringing activities. Most of what we know about the migration of these species is based primarily on field observations and the results of the Migratory Animal Pathological Survey (MAPS) conducted in the 1960s and 1970s. In the 2010s, however, several local ringing projects started. They produced considerable knowledge about the migration of songbirds. More recently, geolocators have also aided researchers in their work, providing even more accurate data on the migratory routes and migratory habits of species. The present study summarises the data we have obtained over the past decade about the migration of long-distance migratory songbirds nesting in North Asia. The article is based primarily on the data collected at ringing stations in the Far Eastern Russia, complemented by research from other areas in East and Southeast Asia. This review highlights the need for further research to ensure long-term protection of species that, at times, show a drastic decline in numbers.

Keywords: East Asian migratory Flyway, songbirds, bird ringing, geolocation, bird migration.

Миграция североазиатских воробьиных

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Аннотация. Восточноазиатско-австралазийская миграционная система птиц является одной из самых богатых видами миграционных систем тем не менее у нас очень мало информации о миграции видов, использующих азиатско-австралазийский пролетный путь. Больше всего известно о водоплавающих птицах (журавли, утки). Однако о певчих птицах известно очень мало, в основном из-за отсутствия крупномасштабных и долгосрочных кольцевых мероприятий. Большая часть того, что мы знаем о миграции этих видов, основана главным образом на полевых наблюдениях и результатах патологоанатомического исследования мигрирующих животных (MAPS), проведенного в 1960-х и 1970-х годах. Однако в 2010- х годах было запущено несколько проектов местного кольцевания. Они позволили получить значительные знания о миграции певчих птиц. Совсем недавно геолокаторы также помогали исследователям в их работе, предоставляя еще более точные данные о миграционных путях и миграционных привычках видов. В настоящем исследовании обобщены данные, полученные нами за последнее десятилетие, о миграции дальних мигрирующих певчих птиц, гнездящихся в Северной Азии. Статья основана в первую очередь на данных, собранных на кольцевых станциях Дальнего Востока России, дополненных исследованиями из других районов Восточной и Юго-Восточной Азии. В этом обзоре подчеркивается необходимость дальнейших исследований для обеспечения долгосрочной защиты видов, численность которых временами резко сокращается.

Ключевые слова: восточноазиатский мигрирующий пролетный путь, певчие птицы, кольцевание птиц, геолокация, миграция птиц.

History of migration studies in East Asia

In Asia, the advent of Western scientists marked the beginning of the in-depth study of nature. They used methods appropriate to the spirit of the given period. Initially, this meant mainly describing, cataloguing and collecting new species. Soon, local trained scientists were also involved. By the time the Japanese Empire was established in the 20th century, Japanese scientists were not only "hunting" for new species, but also comparing what they saw abroad with what they saw at home, and the observation and collection times provided information on the migration of birds in East Asia (McClure 1974). The first local bird ringing programme was also launched in Japan, where between 1924 and 1942, nearly 20,000 birds, mainly ducks, were marked. At the same time, a ringing programme started in the Soviet Union, but it did not cover East Asia (Lebedeva, Shevareva 1964). Based on the available information, possible migration routes were plotted by Tugarinow (1931), Austin (1947; 1949), Hachisuka, Udagawa (1950; 1953), Dorst (1962) and Cheng (1963). The first bird ringing campaign covering a large part of East Asia was only carried out in the 1960s and 1970s. At that time, 1,165,288 individuals of 1,218 bird species were marked within the Migratory Animal Pathological Survey (MAPS), mainly in East Asian countries (McClure 1974). Although the primary aim was to investigate pathogens transmitted by migratory birds, an unprecedented amount of long-term recapture data was also collected. Among songbirds, the largest numbers were of species that could be easily captured in small areas. These were swallows (*Hirundo* spp.) and wagtails (*Motacilla* spp.) that roost in reedbeds. However, this study did not produce much data on the migration of leaf warblers (*Phylloscopus* spp.). Since the 1960s, there have been songbird ringing events in several countries, such as South Korea (Won et al. 1967, Park et al. 2008; Kim 2009; Won et al. 2010; Nam et al. 2011; Moores 2012; Bing et al. 2012; Choi et al. 2013), Japan (Yoshii et al. 1989; Komeda, Ueki 2002; Ozaki 2008; Imanishi et al. 2009), and Russia (Valchuk 2001; Pronkevich et al. 2007; Pronkevich 2011; Heim et al. 2012; Valchuk et al. 2014).

Regular bird surveys have been carried out in the South Primorye area since 1998. The collected data described the migration of several bird species. Valchuk & Yuasa (2002) studied the migration of five species of buntings in the area, while Valchuk & Lelyukhina (2015) used the data from 79,000 individuals of 16 bunting species ringed between 1998 and 2013 to analyse the timing of migration, timing and extent of the species moult, and to identify trends in the population status of migrating birds. Valchuk (2003a; 2003b) showed that Rustic Buntings suspend their migration for moulting. A similar phenomenon was observed by Valchuk & Lelyukhina for the Lanceolated Warbler. The migration of Rustic Bunting was also studied by Valchuk et al. (2005). Lelyukhina & Valchuk (2012) studied the migration of Yellow-browed Warbler between 2000–2011. They provided data on the timing of the species migration in the region, biotopic preferences of birds in the study area, the data on the daily activity of migrants and the duration of their migration stops. Lelyukhina et al. (2015) attempted to identify the origin of Yellow-browed Warblers migrating through the region based on the wing formula. Maslovsky & Valchuk (2015) used the data from 1998 to 2013 to investigate the migration of Siberian Rubythroat, Red-flanked Bluetail and Swinhoe's Robin migrating through the area. Their work included a detailed analysis of the migration periods of the three species. The study also analysed fat accumulation. The local migration of the Siberian Rubythroat has also been studied by Maslovsky et al. (2014; 2018a; 2018b). Among other things, they found an age-dependent migration pattern of the species and that the area was a migration pathway for two different subspecies.

China has a national ringing programme with a tradition of more than three decades (Wang et al. 2006). In South Asia, very few studies have focused on migratory songbirds (e.g. Nisbet 1967; Nisbet, Medway 1972; Round 2010; Ruth et al. 2012). According to Dingle (2004), there are 16 species of songbirds on this migratory route including Arctic Warbler *Phylloscopus borealis* that reaches Sulawesi, the Moluccas and Lesser Sundas Islands, five that reach New Guinea, and none that are regular winterers in Australia.

Yong et al. (2015) reviewed the data about the songbird migration across the East Asian-Australasian Flyway, and focused on 254 species that undertake some latitudinal migration. However, this review reveals that our knowledge of songbird migration is extremely incomplete. Most knowledge still comes from simple field observations, which is particularly true for Leaf Warblers. Since the 2010s, significant progress has been made in the study of songbird migration, thanks to new local ringing surveys and methods. New research sites have been established in Russia (Heim, Smirenski 2013), Mongolia (Davaasuren, 2018), and India (Buner et al. 2015). The tracking data has also provided significant results, as it can be used to learn the exact migration routes of birds. Among the songbirds recorded so far are Black-naped Oriole *Oriolus chinensis*, Pallas's Grasshopper-Warbler *Helopsaltes certhiola*, Red-rumped Swallow *Cecropis daurica japonica*, Yellow-breasted Bunting *Emberiza aureola* (Heim et al. 2020), Siberian Rubythroat *Calliope calliope* (Heim et al. 2018b; 2020), Brown Shrike *Lanius cristatus* (Aoki et al. 2021), Rook *Corvus frugilegus* (Takagi et al. 2014), Willow Warbler *Phylloscopus trochilus yakutensis* (Sokolovskis et al. 2018), Chestnut-cheeked Starling *Agropsar philippensis* (Koike et al. 2016), Chinese Blackbird *Turdus mandarinus* (Choi et al. 2020a), and Stejneger's Stonechat *Saxicola stejnegeri* (Yamaura et al. 2017). All the listed species have been tracked using a range of tracking techniques. Stable isotope analysis of feathers can also help to identify breeding and wintering areas or even migration patterns (Choi, Nam 2011; Weng et al. 2014; de Jong et al. 2019; Choi et al. 2020b). As tracking technologies enable the tagging of smaller bird species, more and more information on species migration and connectivity is becoming available. However, as Yong et al. (2021) point out in a recent review, scientific research needs to continue for conservation reasons, as the populations of many previously common songbird species have declined drastically in recent decades. The only way to resolve this issue is to identify the species migration patterns.

Weather and bird migration

The influence of weather on bird migration in Europe (Alerstam 1978; 1990; Åkesson 1993; Erni et al. 2002; Schaub et al. 2004; van Belle et al. 2007; Arizaga et al. 2011) and in North America (Able 1973; Emlen 1975; Kerlinger, Moore 1989; Deppe et al. 2015) has been studied extensively in recent decades. Siberian species, however, have become the focus of research only recently. It is well known that bird migration is most intense when weather conditions are favourable (windless, clear, anticyclonic weather conditions without precipitation, or with support of tail winds (Alerstam 1990; Gyurácz et al. 1997; Bruderer, Boldt 2001; Erni et al. 2002)). Fabourable weather conditions enhance the orientation of birds, reduce the use of energy for flying and increase the speed of migration (Emlen 1975; Bloch, Bruderer 1982; Gauthreaux 1982; Åkesson 1993; Liechti 2006; Shamoun-Baranes et al. 2017). Weather factors essentially determine the timing of departure from a stopover site (Able 1972; Newton 2007) as well as the direction of migration, the route, the length of flight and the crossing of different ecological barriers (Cochran, Kjos 1985; Weber, Hedenström 2000; Pennycuick, Battley 2003; Cochran, Wikeski 2005; Bowlin, Wikelski 2008; Shamoun-Baranes, van Gasteren 2011; Bulte et al. 2014; Gill et al. 2014). One of the most important weather factors is wind direction, which is a key determinant of migration timing. The most favourable wind direction is the tailwind, which allows birds to travel longer distances with less energy expenditure (Emlen 1975; Bloch, Bruderer 1982; Gauthreaux 1982; 1991; Alerstam 1990; Richardson 1990; Bruderer, Boldt 2001).

The effect of weather on the migration of Siberian songbirds was investigated by Bozó et al. (2018a) and Bozó et al. (under review a) in

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two different geographical regions: the southern shore of Lake Baikal and the Muraviovka Park in the Russian Far East. Both studies involved small insectivorous Leaf Warbler with a body mass of a few grams. Each of the studied species still travels thousands of kilometres between nesting and wintering sites during their autumn and spring migration, which makes them excellent model organisms for analysing the effects of weather on bird migration.

In the Muraviovka Park, the authors used the data from four autumn and four spring migration seasons between 2011 and 2017. The ringing data of four species (Yellow-browed Warbler *Phylloscopus inornatus*, Dusky Warbler *Ph. fuscatus*, Radde's Warbler *Ph. Schwarzi*, and Pallas's Leaf Warbler *Ph. proregulus*) were analysed for a total of 6,191 individuals. The calculations were based on the following variables: minimum and maximum temperature, precipitation, average air pressure, average wind speed and average wind direction. The study compared daily catch totals and the weather factors. The study found that weather is a major determinant of the timing of bird migration—all the species, be it spring or autumn, tend to migrage during warm, calm days without precipitation. The maximum temperature in three out of four species is certainly associated with the timing of migration, as most birds migrated through the area on calm days in both spring and autumn. However, the species showed significant seasonal differences in wind direction. Migration was only intense in autumn during tailwinds (in this case, northern winds), while in spring most birds were trapped during cross winds. The effect of tailwinds was found to be the strongest in Yellow-browed Warbler and Dusky Warbler. This may be one of the drivers of the species migration in Western Europe. Besides, it may provide further evidence for the phenomenon of longitudinal migration. It is very interesting that there was no correlation between air pressure and bird migration, although several studies have shown that the migration peak of most species coincides with days of high air pressure (Alerstam 1990; Gyurácz et al. 1997) due to constant sunshine and low temperatures. Siberian anticyclones with high air pressure and extremely low temperatures form between September and April and are centred in the Lake Baikal region (Oliver 2005). However, it was also highlighted that most of the variation was explained by interannual differences and preferred migration timing, as the studied species are likely to follow their innate migration schedule.

Another study investigated the relationship between weather and bird migration in the southern part of Lake Baikal (Bozó et al. under review a). The two areas differ significantly as the Muraviovka Park does not have large geographical barriers that may affect bird migration, while Lake Baikal, due to its size, is a significant barrier. As a result, different weather factors may affect birds differently. In this study, the data from 2,471 ringed individuals of four species of warblers (Thick-billed Warbler *Arundinax aedon*, Dusky Warbler, Yellow-browed Warbler, and Pallas's Leaf Warbler) were processed during five spring and five autumn seasons between 2015 and 2019. As in the previous study, local nesting individuals and recaptures were ignored. Among the weather factors, daily average temperature, precipitation, average wind speed and wind direction were used to analyse the effects of weather on bird migration timing and their body conditions. In general, the timing of bird migration was mostly influenced by wind strength, as birds migrated mainly in calm weather, similar to the results obtained in the Muraviovka Park. Taking the energy and mortality minimisation strategies into account (Alerstam, Hedenström 1998; Alerstam 1978; Richardson 1978), it is understandable that in strong winds the studied species migrate in significantly smaller numbers than in windless weather. Thick-billed Warbler, a species moving almost in dense vegetation close to the ground in contrast to the forest-dwelling *Phylloscopus*, was found to have no correlation between wind strength and the number of birds trapped. This may be due to the different habitats used by the species. Wind direction was not dominant in either spring or autumn for any of the studied species, which is attributed to easterly winds prevailing in the region (Lutgens, Tarbuck 2001). A similar conclusion was reached by Erni et al. (2002). It was found that birds migrate in central Europe even in unfavourable wind conditions as they do not tend to encounter supporting winds due to the western winds dominating Central Europe. Interestingly, rainfall has no significant effect on the timing of migration. This is understandable in spring when birds migrate to breeding sites to obtain the best possible territories (males) and the best males (females) even in rainy weather. It is difficult to find an explanaiton for the autumn season. Yet, as the authors point out, Leaf Warblers may migrate from tree to tree (short-distance movements) during the day. Thus, the birds are not affected by rain, unlike species that travel long distances. According to personal observations, certain species, such as Buntings, Thrushes and Hawfinches *Coccothraustes coccothraustes*, tend to migrate in large groups on certain days with favourable weather, while Leaf Warblers have been caught in large numbers even on rainy days. The temperature data also contrasted with those obtained in the Muraviovka Park. Yellow-browed Warbler was the only species that revealed a significant correlation between the number of birds and temperature in spring. Unlike most of the studies, the correlation was negative. This may be due to the fact that in spring the dominant easterly winds are typically cold and birds migrate regardless of the temperature. A similar phenomenon was also observed by Richardson (1978) in the northern Yukon area.

This study also looked at the fat reserves and body mass of birds migrating during different weather conditions. It showed that birds migrated with very low fat reserves in both spring and autumn, which was influenced by temperature, precipitation, wind direction and wind strength. In case of low temperature, birds were in better conditions, had more fat and weight, which is only natural as, in general, low temperature increases the energy requirements of birds (Richardson 1978). During stronger winds and tailwinds birds also increased their body mass and fat reserves. Birds need less energy to cover the same distance under supporting winds (Tucker 1974; Alerstam 1976). For species crossing large barriers along their migratory journey, sufficient fat reserves and tailwinds are essential (Berger, Hart 1974; Tucker 1974). In addition, especially in spring and in case of species breeding in northern latitudes, high fat reserves are crucial, since these species often arrive to the breeding grounds very early when the food availibility is poor (Ryder 1971; Irving 2012). Moreover, strong winds increase heat loss, therefore, high fat reserves are essential (Richardson 1978). This is the reason why Thick-billed Warblers and Pallas's Leaf Warblers have more fat on rainy days.

However, when examining weather factors, it should also be noted that no ringing was observed at any of the sites in strong winds or heavy rainfall, so these extreme events, which significantly affect bird migration, were not investigated. As pointed out by Lövei et al. (2001), capture probability varies by species and movement height. It is also added that smaller species have a superior manoeuvring capability and, thus, are very likely to avoid capture. For this reason, it is conceivable that the probability of catching decreases due to strong winds, so the wind strength distorts the results.

Migration directions: Loop migration and longitudinal migration

Some of the bird species do not use the same routes for spring and autumn migration because of the seasonal differences in prevailing winds during migration and/or variation in food availability (Gauthreaux et al. 2006; Shaffer et al. 2006; Klaassen et al. 2011; Thorup et al. 2017; Tøttrup et al. 2017). This migration pattern is called loop migration, and a number of bird species in different migration systems use this strategy (Phillips 1975; Gill et al. 2009; Klaassen et al. 2010; Szép et al. 2017; Tøttrup et al. 2017). Loop migration has been detected mainly from recaptures and the data on birds tagged with different tracking techniques. However, due to the

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very small number of long-term recaptures in the East Asian migration system and the low number of species tagged with different tracking devices (e.g. Yong et al. 2021), this cannot be studied at present. The question of whether there are any species of Siberian songbirds that are characterized by loop migration can only be answered with biometric data. It is known that the size and shape of the migratory loop may differ between populations (Newton 2007), and that wing length may also differ between populations within species and between geographical regions, as northern populations migrate longer distances, which requires longer, more pointed wings (Mönkkönen 1995; Pérez-Tris, Tellería 2001; Arizaga et al. 2006; Nowakowski et al. 2014). Therefore, if a ringing station is operated in both spring and autumn, it is possible to compare the wing lengths of adult birds migrating through the two seasons and possible differences may be indicative of loop migration (Ozarowska et al. 2011; Jónás et al. 2018). This method was applied by Bozó et al. (2020) to study loop migration using the data from the ringing stations on the southern shore of Lake Baikal and in the Muraviovka Park, 1,500 km east of Lake Baikal. The authors had previously assumed that these species migrate along the same route in spring and autumn, as they are not assumed to fly over high mountain ranges, but migrate over their entire range near the East Asian coastal zone (despite the fact that several species have been shown to fly over even the highest mountain ranges). They analysed the data on 2,368 ringed adult individuals of six songbird species (Red-flanked Bluetail *Tarsiger cyanurus*, Siberian Rubythroat, Taiga Flycatcher *Ficedula albicilla*, Arctic Warbler, Thick-billed Warbler and Black-faced Bunting *Emberiza spodocephala*) (for the exact methodology see Jónás et al. 2018). Their results essentially supported their null hypothesis, i.e., no difference in wing length was found between spring and autumn for most species, suggesting that these species were not loop migrants. This may be due to the adequate food supply and similar prevailing wind directions for birds in both spring and autumn seasons, and the lack of obvious ecological barriers that have to be crossed during migration along the East Asian Flyway. Previously, Heim et al. (2018b) also found no indication of loop migration in the Siberian Rubythroat, but leapfrog migration (populations breeding further north overwinter further south) has been detected in this species using stable isotope analysis (Weng et al. 2014). However, in the case of Red-flanked Bluetail and Black-faced Bunting, it is conceivable that either males or females used different routes in spring and autumn. The only direct evidence is a male Red-flanked Bluetail that was ringed in the Muraviovka Park in spring 2015 and then captured in Lake Baikal in autumn 2015. However, this may also be an example of longitudinal migration. It is worth noting that the wing length differed between years, which may be due to the fact, that if weather and feeding conditions are unfavourable, birds may invest less energy in moulting, and, therefore, feather length and the duration of the moulting period will change (Pienkowski, Minton 1973; Heitmeyer 1987).

In conclusion, it can be said that further research is needed to clarify the issue, because the obtained results and the methodology behind the study raise several questions. However, the currently available geolocator data support the obtained results and show that Siberian songbirds are not characterised by loop migration.

Another long studied issue is the longitudinal migration strategy of bird species wintering in Southeast Asia and nesting in Northern Eurasia. Presumably, songbird species nesting in the west do not fly through the mountainous regions of Central Asia, instead, they initially head east and then turn south close to the East Asian coast thus avoiding the major barriers. This possibility was raised by Tugarinow (1931) in relation to Asian migration routes. This migration route for certain species is also mentioned by McClure (1974). Some species that had previously nested only in the east began to expand westwards. New populations, sometimes nesting thousands of kilometres away from their original range, continued to use ancestral wintering grounds and routes rather than joining the Eurasia-Africa migration system. McClure (1974), following Timofeeff-Ressovsky (1940), gives an example of Yellow-breasted Bunting, which gradually expanded westwards from the mid-19th century onwards. However, European populations that followed this trend still used traditional wintering sites. These data are obtanied from recaptures of ringed individuals, but it is also possible to study longitudinal migration using other methods such as biometrics and tracking data. In recent years, tracking systems have been applied to several songbird species in the East Asian bird migration system. This primarily refers to the birds marked in the Russian Far East, Japan, and Korea, unlike individuals from more western populations. This means that longitudinal migration could not be detected. However, Bozó et al. (in prep.) found clear evidence in support of the hypothesis. They studied different warbler species based on the biometric data collected in two geographical regions. The study was conducted on a total of 11,921 individuals in the southern part of Lake Baikal and in the Russian Far East, the Muraviovka Park, and included nine species (Arctic Warbler, Two-barred Warbler *Ph. plumbeitarsus*, Pallas's Leaf Warbler, Yellow-browed Warbler, Dusky Warbler, Radde's Warbler, Thick-billed Warbler, and Pallas's Grasshopper Warbler). The study compared the timing of spring and autumn migration of birds migrating through the two sites in both seasons. The results show that in spring most species migrated significantly earlier east than in Lake Baikal, some 1,500 km to the west, and in autumn the opposite pattern was observed. This was attributed to the weather and the nesting habits of the species: in the area around Lake Baikal (and thus in much of Siberia) spring comes much later than in the Muraviovka Park, and species nesting in herbaceous vegetation can only build nests after the weather has become more favourable. Dusky Warbler, however, is not associated with herbaceous vegetation (Forstmeier 2002), and, therefore, it is not by chance that in spring it arrives in the Muraviovka Park the first among the studied species. It has also been shown that the migration periods in Lake Baikal are much shorter than in the Muraviovka Park, which may also be due to weather differences.

Results from geolocator-tagged individuals from different nesting populations of different songbird species from western to far eastern Russia will be published in the near future (Heim et al. pers. comm.). These results also support the longitudinal migration theory, however, as highlighted by several authors (Delany et al. 2017; Han et al. 2017), some species are able to fly across even the largest geographical barriers, such as the Gobi and the Himalayas. For example, the capture-recapture data have provided evidence that ducks can fly across higher mountain ranges of Central Asia to wintering grounds in India (McClure 1974). Similarly, some species near wintering grounds may cross uplands and mountains in central and southern China and the Northern Indochina (Tordoff 2002; Fei et al. 2015). For this reason, it would be necessary to equip individuals from as many populations of as many species as possible with geolocators, as different species are likely to use different strategies.

Sex-specific migration and factors controlling migration phenology

In addition to differences between species, the migration of males and females may also differ due to the different distance of the wintering grounds for a particular sex, their earlier departure from the wintering grounds or faster migration (Morbey, Ydenberg 2001; Coppack, Pulido 2009; Schmaljohann et al. 2016; Woodworth et al. 2016; Briedis et al. 2019; Schmaljohann 2019). Songbirds tend to exhibit protandry in spring (Morbey, Ydenberg 2001), i.e., males arrive at nesting sites earlier than females. The reason for spring protandry is that males need to return early in spring to occupy a suitable territory, which is driven by sexual selection pressures (Reynolds et al. 1986; Coppack et al 2006). Spring protandry has been detected in several species in different migratory systems (Durman 1967; Lawn 1974; Reynolds 1978; Spina et al.

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1994; Rubolini et al. 2004; Harnos et al. 2015). In autumn, however, protandry is typical of migratory species, as females leave breeding sites earlier than males that either stay longer (Logan, Hyatt 1991; Weggler 2000) or search for new nesting sites (Forstmeier 2002; Mills 2005). In recent years, several studies have investigated the sex-dependent migration of songbirds in the East Asian migratory system. The studies found that many songbird species follow this migration pattern. Bozó & Heim (2016) studied the sex-specific migration of seven *Phylloscopus* species (Dusky Warbler, Radde's Warbler, Pallas's Leaf Warbler, Yellow-browed Warbler, Arctic Warbler, Two-barred Warbler, and Pale-legged Leaf Warbler *Ph. tenellipes*) in the Muraviovka Park using the biometric data (wing length and length of the 3rd primary feather) from 6,287 individuals. The study found that the wing lengths of four species — the Dusky Warbler, Radde's Warbler, Pallas's Leaf Warbler, and Yellow-browed Warbler—showed a bimodal distribution with shorter-winged birds migrating later in spring and earlier in autumn than longer-winged birds. They considered this to be evidence of sex-specific migration, since it is also typical of European Leaf Warblers (Durman 1967; Lawn 1974; Reynolds 1978). They also ruled out the possibility that these birds came from different populations or that the bimodal distribution was due to different timing of migration between age groups. At the same ringing station, Wobker et al. (2021) conducted a multi-species analysis that partially addressed this issue. In their work, 12 species had enough ringed individuals to investigate sex-specific migration. The study found that half of the species showed spring protandry (Red-flanked Bluetail, Mugimaki Flycatcher *Ficedula mugimaki*, Taiga Flycatcher, Brambling *Fringilla montifringilla*, Little Bunting *Emberiza pusilla*, and Yellow-throated Bunting *E. elegans*), while the remaining species (Brown Shrike, Grey-backed Thrush *T. hortulorum*, Dusky Thrush *T. eunomus*, Rustic Bunting *E.*, and Pallas's Reed Bunting *E. pallasi*) did not show significant sex-dependent differences in migration timing. The extent of protandry was found to be 2–9 days. In the autumn, 14 species were analysed (the species mentioned above plus Naumann's Thrush *T. naumanni*, Bluethroat *L. svecica*, Common Rosefinch *Carpodacus erythrinus*, Common Redpoll *Acanthis flammea*, and Chestnut Bunting *E. rutila*). Of them, three species (Brambling, Rustic Bunting, and Pallas's Reed Bunting) showed protogyny and one species (Yellow-throated Bunting) showed protandry. The study concludes that sex-differentiated migration may be a general phenomenon in this migratory system, but not necessarily at the species level, but rather at the population level. Nam et al. (2011) also confirmed that sex-specific migration is a common phenomenon along this route. The conclusion was based on the data collected at a ringing station in Korea between 2006 and 2008 from 940 individuals of five bunting species (Yellow-browed Bunting *E. chrysophrys*, Chestnut Bunting, Black-faced Bunting, Tristram's Bunting *E. tristrami*, Yellow-throated Bunting). Five species revealed a pattern where, in spring, males returned on average 6.3 days earlier than females. Bozó et al. (in prep.) processed the data from 8,334 individuals of 11 species (Common Rosefinch, Hawfinch, Little Bunting, Black-faced Bunting, Taiga Flycatcher, Brown Shrike, Siberian Rubythroat, Eurasian Siskin *Spinus spinus*, Red-flanked Bluetail, Dusky Thrush, and Naumann's Thrush) in Lake Baikal during the autumn and spring seasons of 2014–2018. Their results are similar to those of the papers presented so far. Namely, the studied species show protandry in spring and protogyny in autumn migration. In the spring, males arrived significantly earlier than females in the case of Common Rosefinch, Little Bunting, Black-faced Bunting, Taiga Flycatcher, Brown Shrike, Siberian Rubythroat, and Red-flanked Bluetail, while there was no significant difference in the arrival of females in the other species. In the autumn, Hawfinch, Taiga Flycatcher, Brown Shrike, and Red-flanked Bluetail males arrived later than females. Again, the differences were greater in spring than in autumn.

Thus, the studies presented here clearly show that sex-dependent migration is common for the East Asian migration system. However, in addition to sex-related factors, other factors, both external and internal, also determine the timing of species migration. Among them are age, migration distance (Marchetti et al. 1995; Jenni, Kéry 2003), moult strategy (Pulido, Coppack 2004), and feeding patterns (Katti, Price 2003). In recent years, several studies in the Muraviovka Park and Lake Baikal have investigated factors influencing migration. The first to address this issue was Bozó et al. (2021). Their work used the data collected between 2013 and 2017 from 9,211 ringed individuals of 7 warbler species (Yellow-browed Warbler, Arctic Warbler, Two-barred Warbler, Pale-legged Leaf Warbler, Dusky Warbler, Radde's Warbler, and Pallas's Leaf Warbler). They found that migration phenology of these species was related to moult, the size of their preferred prey in spring, and the position of their southernmost wintering areas in autumn. The relationship between moulting and migration timing has been highlighted in other studies as well (Owen, Krohn 1973; Kjellén 1994; Pérez-Tris et al. 2001; Pulido, Coppack 2004). The moulting strategy (winter or summer complete moult) may also influence the timing of spring migration. Spring migration might be delayed in species moulting in winter (as in the case of Two-barred Warbler and Arctic Warbler in the study under consideration)—species replacing flight feathers during winter may delay departure compared to species that moult in summer (Rubolini et al. 2005). Food size also correlates with the time of spring return, which, as is assumed by the authors, is due to the avilability of smaller-sized-food earlier in the spring, allowing smaller species to return earlier. In terms of migration distance, they found that the species that overwintered in the autumn were the earliest to leave the study site, while in spring they were the latest to return. It is important to note, however, that the length of the breeding season has no effect on the timing of migration, probably because short summers mean that each species breeds only once a year, so the species show no difference in this respect. A similar analysis has been carried out by Wobker et al. (2021). Their results show that, in addition to migration distance and molt strategy, another factor that determines the timing of migration is age. Specifically, the effects of age "were associated with the birds' molt strategy and the mean latitudinal distances from the assumed breeding area to the study site". They found that adult species with postnuptial moult passed the study site later than first-year birds undergoing only a partial molt. This pattern, however, reversed with an increase in the migration distance to the study site. In autumn, 11 of the 25 species studied showed an effect of age on the timing of migration (typically adult birds migrated through the area earlier), while in spring this was only the case for two of the eight studied species (Red-flanked Bluetail and Taiga Flycatcher) (again, adult birds arrived earlier than young birds). In spring, adult birds may have returned earlier than young birds because they are more experienced than young birds. In autumn, it is also a common phenomenon in other migration systems for species performing complete molt in winter (Carlisle et al. 2005; Kiat, Izhaki 2016), while young birds performing only partial molt before the onset of autumn migration migrate ahead of the adult summer molters when their mean breeding latitude is relatively close to the study site.

The third study carried out in Lake Baikal by Bozó et al. (in prep.) also investigated the factors influencing migration in several species. Their results showed that in spring, in addition to the age of birds (adults returned earlier), the migration period correlated with the type of food (seed-eaters returned later than insect-eaters) and the timing of molt (those that have complete moult in winter came later). However, the study found no correlation with migration distance. In the autumn, in addition to sex-related factors, migration timing depended on migration distance (the shorter the migration distance, the later they arrive), food (seed-eaters migrate earlier than insectivorous species) and molt (summer molters

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migrate later). Autumn migration timing did not reveal any correlaiton with age. An interesting finding was that in the spring, some insectivorous species migrated through the area earlier than seed-eaters, which was attributed to the difference in range size. In particular, in the case of Red-flanked Bluetail, individuals from the westernmost populations need to migrate to the breeding sites very early in spring even under less favourable feeding conditions. Similar to the results of the previous study, adult birds migrated through the area earlier in both spring and autumn. Although the results were not significant, it was found that species with longer migration routes migrated later in spring and earlier in autumn. Overall, the results of this study are similar to those of the previous ones, and it can be clearly stated that the timing of migration in this migration system is influenced by the factors similar to the other systems.

Migration strategies and stopover ecology of Siberian Passerines

Most bird species cannot cover the entire migration distance in a single flight and have to take rest stops (Schaub, Jenni 2001). The number of times a bird species stops to rest and feed during migration is influenced by several factors, often resulting in different migration strategies for different species. The migration strategy is largely determined by the amount of time birds spend at resting sites and the amount of reserved "fuel" they can accumulate during this time (Alerstam, Lindström 1990; Lindström, Alerstam 1992; Alerstam, Hedenström 1998; Schaub, Jenni 2001; Arizaga et al. 2008). Some species migrate with high fat reserves and can thus travel longer distances (e.g., Marsh Warbler *Acrocephalus palustris*) (Csörgő, Gyurácz 2009), while others, such as Savi's Warbler *Locustella luscinioides*, have low fat reserves, which makes them stay longer at the stopover site and migrate faster over shorter distances (Neto et al. 2008). As the stopover ecology of birds can be studied at localised ringing sites without the need for a large geographical network, several studies on the East Asian Flyway have been conducted earlier, however, the most intensive research on this topic also comes from East Russia from recent decades (Bozó et al. 2018b; Heim et al. 2018b; Bozó et al. 2019b; 2019c; Sander et al. 2020) or China (Wang et al. 2006). Bozó et al. (2020) compared the stopover ecology of Yellow-browed Warbler and Red-flanked Bluetail in the Muraviovka Park. In their work, they processed the data from 6,073 ringed and 502 recaptured birds. In general, they found slight differences in body mass gain between the two species, but no significant differences in stopover duration. For Red-flanked Bluetail the minimum stopover duration averaged 3.4 days in the autumn and 1.7 days in the spring, while for Yellow-browed Warbler it was 3.2 days in the autumn and 2.1 days in the spring. Shorter stopover times have been described for both species in the spring, suggesting that, unlike in the autumn, both species might follow a time-minimizing strategy in spring season. Wang et al. (2006) obtained similar results for Red-flanked Bluetails in North East China. They highlighted that males spent longer time in the stopover site than females in both seasons. However, there was also a significant difference between the results of the two studies, namely, in terms of minimum stopover duration, with birds staying longer at the Chinese stopover site (5.7±4.3 days in the autumn and 3.4±3.4 days in the spring). This was attributed to the difference in habitats, with the higher proportion of shrubland habitats more favourable to the species, which meant that birds in the Muraviovka Park refueled more quickly. A stopover duration similar to that of European species was found for Yellow-browed Warbler. For the insectivorous Yellow-browed Warbler, stopover duration increased in autumn as time progressed, which the authors explain by a decrease in food availability. In relation to refuelling, they found that the body mass of Red-flanked Bluetails significantly increased during stopovers in the spring and autumn, while Yellow-browed Warblers showed an increase in spring. The increase in body mass (4.1%) in the spring compared to 0.9% in the autumn of recaptured Yellow-browed Warblers clearly supports the idea that birds migrate faster in the spring and accumulate more reserves over a shorter time. Interestingly, in the case of Red-flanked Bluetail in China, Wang et al. (2006) found sex-specific differences in the body mass change: during the stopover females gained mass (4.7%), while males lost mass (–1.5%). In that study, a total of 2,435 Red-flanked Bluetails were ringed during an autumn and a spring migration period. A body weight gain of 1 g/day was observed in the recaptured birds. Body weight gain was much higher in males than in females in spring, which is due to the fact that males migrate faster to the breeding sites. Females spent more time in the area, that suggests that females may have to stay longer to gain energy stores for further migration.

Sander et al. (2020) investigated the autumn energy storage of 10 different species of warblers (genera *Acrocephalus*, *Arundinax*, *Locustella* and *Phylloscopus*) in the Muraviovka Park. Their results show that some species, such as Pallas's Leaf Warbler carries more fat, fuelling longer flight bouts with fewer stops, while others, such as Thick-billed Warbler, carry less fat and require more frequent stopovers on migration. Most species also increased their energy stores within days and within seasons.

Bozó et al. (2019c) investigated the migration of Pallas's Grasshopper Warbler and Lanceolated Warbler *Locustella lanceolata* in the Muraviovka Park using the data from 841 individuals. They found, that the recaptured Pallas's Grasshopper Warblers had an average of 5.3 ± 6.9 day stopover in the autumn without any significant change in their body mass. In case of Lanceolated Warblers, in autumn on average 6.7 ± 5.5 days elapsed between the first and the last capture and there was no significant change in body mass during the stopover. Therefore, the migration strategies of these species are similar to that of Savi's Warbler *L. luscinioides*, namely, fast migration without long-term stopovers. It has also been shown that the timing of molting has a profound effect on the timing of bird migration and the differences between the timing of migration for young and adult birds.

Passerine migrants are known to use a range of habitats at stopover sites that are much wider than those occupied during the breeding season (Bairlein 1983; Bilcke 1984; Chernetsov 2006), however, they still have species-specific habitat preferences (Bairlein 1983). In the East Asian migratory system, Bozó et al. (2018b) investigated the stopover habitats used by warblers (genus *Phylloscopus*, *Acrocephalus*, *Arundinax*, and *Locustella*), while Heim et al. (2018a) investigated the stopover habitats used by buntings (*Emberiza* spp.) in the Muraviovka Park. In general, Bozó et al. (2018b) found that most species exhibit species-specific preferences for the type of habitat. They also noted that these stopover habitats were similar to the habitats used as breeding grounds. Presumably, certain species prefer certain habitats over the others due to different eating habits and foraging patterns. They also found that disturbed, ruderal habitats were not favourable for the birds. In contrast, Heim et al. (2018a) found that during migration most bunting species occur in diverse habitats. In the spring, wetland habitats were found to be of lesser importance for the studied species, probably, because these habitats do not provide adequate foraging opportunities in the spring. In the autumn, on the other hand, birds were typically found in habitats where they occurred during the breeding season, especially in wetland habitats.

Migration routes: Satellite tracking, geolocators, stable isotopes, citizien science data and flight range estimation by biometric parameters

In recent years, a growing number of songbird species using the East Asian migratory system have been tracked by a range of tools to map their migration routes (e.g. Heim et al. 2020). Such systems, however, have only been used for certain body sizes. In the case of the smallest-sized long-distance migratory species, the *Phylloscopus* species, only the East Asian subspecies of the Willow Warbler has been studied by geolocators. Along with that, this species does not migrate along the

East Asian route, rather, it flies across Central Asia to reach its wintering grounds in Africa (Sokolovskis et al. 2018). Due to the technical challenges, other methods were used in the past to try to identify the routes that birds take to reach wintering sites and their exact location.

Clearly the "oldest" but the most accurate way to address this issue is to use the capture-recapture method. Yet, it yielded very few results in East Asia due to the lack of organised large-scale ringing. Perhaps, the most comprehensive study was carried out during the MAPS programme in the 1960s and 1970s, when over 1 million birds were ringed. However, a relatively large numbers of recaptures included mainly ducks, which are popular with hunters, and larger bodied shorebirds (McClure 1974). Songbirds were also under-represented in that study. Long-term recaptures were effective only for Red-rumped Swallow, Barn Swallow *Hirundo rustica*, Brown Thrush *T. chrysolavs*, Tree Pipit *Anthus trivialis*, Forest Wagtail *Dendronanthus indicus*, White Wagtail *Motacilla alba*, Yellow Wagtail *M. flava*, Brown Shrike, European Starling *Sturnus vulgaris*, Common Rosefinch, Hawfinch, Yellow-breasted Bunting, Chestnut Bunting, and Black-faced Bunting. So, in most cases, species were ringed in large numbers in reedbeds where they stayed overnight and recaptured in similar habitats where they overwintered. Based on the recapture data, the East Asian migratory system has two migratory pathways. This was later confirmed by the data on birds equipped with geolocators and transmitters (Higuchi 2005; Yamazaki et al. 2012; Concepcion 2017; Heim et al. 2020). The first is the 'island' or 'oceanic' route linking eastern Russia (Kamchatka and Sakhalin) and Japan to the Philippines and eastern Indonesia, and the second, the 'mainland' route, is the one linking eastern Russia, China, and continental Southeast Asia. It can be seen that for some long-distance migratory bird families, such as warblers, flycatchers, small thrushes, etc., no long-term recaptures were available during this period. This is probably because these species could not be marked in the same numbers as swallows or wagtails, and so the chances of recaptures were much lower. It is also possible that not all the species use the two routes. They may only be used by those with specific habitat requirements (roosting in reedbeds) for which this theory was proposed. However, it should be noted that, for example, in the case of Pallas's Grasshopper-Warbler (Nisbet 1967) or Oriental Reed Warbler *A. orientalis* (Nisbet, Medway 1972), the MAPS programme resulted in a significant number of year-to-year recapture records at wintering sites. This generated the insights into the wintering-site ecology of these species. After the MAPS programme, a ringing network covering the whole of eastern Asia was not established, so long-term recaptures were not achieved. Although local ringing stations were established in several countries of the region in the 2010s (reviewed in Yong et al. 2015), their location is patchy and only minimal long-term recapture data are available. The recapture data for some species are also described in Heim et al. (2020). Their study also shows under- or even over-representation of some species.

In the absence of recaptures, other methods are needed to identify migration routes, wintering and nesting sites. The most cost-effective method is to estimate flight distances based on biometric parameters. This approach has been applied to warblers by Sander et al. (2017) and Bozó et al. (2019b). This method is based on measurable parameters such as body mass, body fat and body muscle (Delingat et al. 2008; Arizaga et al. 2013). Sander et al. (2017) estimated flight distances in the Muraviovka Park in the Russian Far East, while Bozó et al. (2019b) estimated flight distances for leaf warblers migrating through the southern part of Lake Baikal (see the aforementioned articles for the methodology of the study). The main conclusion was that in different points of Siberia, individuals of certain species use a similar strategy in terms of the distance travelled and number of stopover sites used in migration, while for other species, geographical features may cause significant differences in the migration strategy. The flight ranges of Pallas's

Leaf-Warbler (724 km) and Radde's Warbler (510 km) estimated by Bozó et al. (2019b) were similar to those of birds studied by Sander et al. (2017), and the number of calculated stopovers was also similar between the two areas (8–10 stopover). In contrast, Dusky Warbler trapped at Lake Baikal were estimated to fly shorter distances (217 km) and therefore must have stopped more frequently on their way to the wintering grounds (17–18 times). Bozó et al. (2019b) attributed the differences in the two areas to different geographic conditions.

In addition to the ringing data, modern technologies can also be used to track the origin of birds. Stable hydrogen isotope analysis has already been carried out in the East Asian migratory system for several bird species, including various waterbird species (Bar-headed Geese *Anser indicus*, Whooper Swans *Cygnus cygnus*, Mongolian Gulls *Larus vegae mongolicus*, Curlew Sandpipers *Calidris ferruginea*, and Pacific Golden Plover *Pluvialis fulva* (Pérez et al. 2010); Great Cormorant *Phalacrocorax carbo* (Chang et al. 2008)) or Siberian Rubythroat (Weng et al. 2014). In the Siberian Rubythroat, Weng et al. (2014) found that individuals from more northerly populations winter further south, while individuals from more southerly populations winter further north (leapfrog migration). In this study, stable hydrogen isotope analysis of feathers was performed on 56 Rubythroats trapped or found in bird markets in Taiwan (see the method there). Since adult birds perform complete and young birds partial moult at breeding sites, the δDf values of the rectrices should reflect the δDp of the breeding region. The method is mainly used to determine the latitude along which the birds have grown their feathers, but it is not suitable for determining the exact place of origin (Hobson, Wassenaar 1997). A more complex isotopic analysis would be needed to identify this, as emphasised by de Jong et al. (2019). Similarly to Weng et al. (2014), de Jong et al. (2019) found that Yellow-browed Warbler birds migrating in Western Europe may originate from a very wide breeding range. This was showed by the stable hydrogen isotope analysis.

More reliable, but far from accurate, results can be obtained with geolocators that can be fitted to smaller species, as the precision of the location estimates varies strongly due to shading by vegetation, bird behaviour, length of stay at a given site and time of the year (Lisovski et al. 2012). However, in recent years this tracking technique has been applied to a number of species and the first results have been published. The first passerine species in the East Asian Flyway that has been marked with light-level geolocator was Chestnut-crowned Starling (Koike et al. 2016). The species breeds in Japan and spends the winter in Southeast Asia. The authors suggest that the reason for the advanced breeding season is due to the changes in migration and wintering patterns related to temperature. However, no information on the migration of the species was previously available, so a total of 70 adult birds were geolocated in central Japan in 2012 and 2013, of which 16 provided data. The study produced the data on migration timing, the location of migration routes and wintering sites, the location and length of stopovers and the duration of migration. It was found, among other things, that some of the birds spent the winter in Borneo and others in the Philippines, using the "island route" during their migration. They left the breeding grounds in September and arrived at the wintering grounds by the end of October, from where they left for the breeding grounds at the end of March.

After Chestnut-cheeked Starling, the migration of Stejneger's Stonechat was investigated using light-level geolocators (Yamaura et al. 2017). Their work identified the migratory routes, migration stopover sites, and major non-breeding grounds based on geolocator data from 12 individuals nesting in Hokkaido. 30% (14 individuals) of the 46 birds fitted with geolocators in 2014 returned in 2015, of which 12 provided data. All the individuals were found to have reached southeast Asia via the southern Primorye in the South of the Russian Far East or eastern Heilongjiang. This is a fundamental difference from the previous study, and may be attributed to the fact

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that grassland species colonised Japan from the mainland during the last ice age, and the link has persisted to the present day. On average, the birds made 3.6 stopovers in their migration, reaching wintering sites in southern China and mainland Southeast Asia in early December.

In 2018, the first study from the Russian Far East was published. It explored the migration of Siberian Rubythroat using light-level geolocators (Heim et al. 2018b). A major problem was that the study was based on a low sample size (3 birds) and was highly selective (only adult males). It was found that departure from both wintering sites and nesting sites identified from southern China to Cambodia depended on vegetation greenness: birds left areas with decreasing vegetation greenness. In spring and autumn, one stopover site was identified in China. The migration of birds was not characterised by major detours (for example, loop migration) in either season, but their spring migration route was slightly more easterly than in the autumn.

Heim et al. (2020) conducted a study to validate the seasonal distributions by citizen science data of eight species (Chestnut-cheeked Starling, Siberian Rubythroat, Red-rumped Swallow, Yellow-breasted Bunting, Barn Swallow, Pallas's Grasshopper-warbler, Black-naped Oriole, and Stejneger's Stonechat) based on the geolocator data and long-term recaptures. In general, they found that the combination of different types of data provides a suitable opportunity to study the birds' distribution beyond breeding season and migration connectivity. Another important finding of this paper was that the extent of wintering grounds may be smaller than that the currently available distribution maps indicate. The geolocator-tagged species typically did not follow the East Asian coast, with Siberian Rubythroat, for example, migrating significantly further west into the mountainous areas of China. However, the study confirmed the two hypothesised migration routes (inland China and islands). Migration connectivity could only be investigated for two species due to the limited data available, and was found to be high for both Siberian Rubythroat and Barn Swallow.

The importance of citizen science data in migration research was also highlighted by Bozó et al. (under review b). In this work, they collected available published occurrence data on eight species of warblers (genus *Phylloscopus*, *Arundinax* and *Locustella*) and used observational data uploaded to the eBird database to find out the period of the year and the geographical regions of the birds' presense. Based on the data, it was concluded that most of the species under study migrate faster in spring than in autumn. It was also found that these species are most likely leapfrog migrants. There are several observational data during the breeding season period in their wintering areas, which is probably due to the intensive birding activities in South and Southeast Asia. For the two *Locustella* species (Lanceolated Warbler and Pallas's Grasshopper-Warbler) it was assumed that there is an important stopover site along 25° N close to the East Asian coast. However, there are also observations from the wintering sites for some species during the breeding season, which could certainly be related to injured birds.

The results of the latter two studies highlight the fact that citizen science data can be of great importance for a better understanding of bird migration in otherwise data-poor areas, but may also raise questions of credibility. A data set can only be considered credible if a photo or audio record of the species is made, but, mostly, this is not the case. It is therefore preferable to use species data from online databases where field identification is clear and simple and the potential for misidentification is minimal.

Looking to the future: The importance of basic research for the protection of species

The topics covered in this paper have given us an insight into the current status of migration research on songbird species using the East Asian Flyway. We have seen that, compared to the 20th century, the last decade has seen significant advances in the understanding of long-distance migratory songbird species. However, there is still a significant knowledge gap compared to, for example, the American or the Palearctic-African migratory systems. The primary reason for this is the lack of an organised ringing network covering the whole migration route. There are some well-established ringing stations, yet, long-distance recaptures require a whole network of those. This gap can now be filled by the use of modern technology. Besides, an increasing popularity of birdwatching as a hobby in the region can also provide a significant amount of data. There is an urgent need to consolidate all the tools and efforts to learn more about the migration of species, as recent studies have shown drastic declines in the populations of many bird species. A prime example is Yellow-breasted Bunting, now regarded as an umbrella species by researchers (Heim et al. 2021). A population survey conducted in Hokkeido, Japan, in 2002 and 2003 showed a drastic decline in the population of this species compared to the 1970s and 1980s. This is also true for Eurasian Skylark *Alauda arvensis* and Lanceolated Warbler (Tamada et al. 2017). Similar local population declines have occurred in Central Siberia (Bourski 2015), at Lake Baikal (Mlikovsky, Styblo 2016) or in the Russian Far East (Antonov 2016). In a literature review, Kamp et al. (2015) collected published data on the decline of the species and came to a quite striking conclusion. The population of this species with a vast range declined by 84.3–94.7% between 1980 and 2013, and the species' range contracted by 5,000 km. This unimaginable decline is mainly due to illegal capture of birds for consumption and trade on migration routes and wintering grounds, as exemplified by the fact that in one province of China, approximately 1 million individuals were consumed in a single year (Chan 2004). A similar data analysis for Rustic Bunting reveals a 75–87% decline in overall population size over the last 30 years and a 32–91% decline over the last 10 years (Edenius et al. 2017). Meanwhile, Yellow-breasted Bunting has been placed in the highest conservation category in China. This may be the reason why in some parts of the nesting range the species is again showing an increase in population (Heim et al. 2021).

Yellow-breasted Bunting is an excellent example of the need to identify the migration routes, stopover sites, and wintering grounds of a species, and to understand the migration ecology in order to protect it. This is, by far, the only way to understand the causes behind the population decline. Future basic research should, therefore, be continued, as not only the spectacular species are negatively affected by illegal trade, hunting and habitat destruction, but also the less spectacular ones (Yong et al. 2015; 2021).

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