

Seasonal morphological differences indicate possible loop migration in two, but not in another four, Siberian passerines

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Loop migration, i.e. the use of different routes during spring and autumn migration, is a common migratory strategy among many long-distance migratory species. This migration strategy is most likely driven by the variation in food availability and/or prevailing winds en route between the spring and autumn seasons. Tracking studies and long-distance ring recoveries have revealed that many of the species that migrate along the American and Eurasian–African migratory flyways use different stopover sites in spring and in autumn. However, very little information is available on songbirds migrating along the East Asian flyway. In this study, we compared the wing lengths of six East Asian long-distance migratory passerines (Red-flanked Bluetail *Tarsiger cyanurus*, Siberian Rubythroat *Calliope calliope*, Taiga Flycatcher *Ficedula albicilla*, Arctic Warbler *Phylloscopus borealis*, Thick-billed Warbler *Arundinax aedon* and Black-faced Bunting *Emberiza spodocephala*) migrating through two different study sites in Russia. We examined whether these species show morphological differences between spring and autumn migration which could indicate the occurrence of different populations at different parts of the migratory cycle. Based on a dataset of 2,368 adult individuals, we found no differences in wing length between the two seasons for four studied species, suggesting the absence of loop migration. This might be explained by adequate food supply and similar prevailing wind directions for birds in both spring and autumn, or the lack of obvious ecological barriers along the East Asian flyway which have to be crossed during migration. However, the differing wing lengths of individuals captured in spring and autumn for two species, Black-faced Bunting and Red-flanked Bluetail, provide evidence for the possible use of different seasonal migratory routes. Further field studies are needed to better understand the migration ecology of passerine birds in the East Asian flyway.

INTRODUCTION

Every year, billions of songbirds migrate thousands of kilometres between temperate breeding sites and the tropics as a natural part of their annual cycle (Newton 2008). Many birds do not use the same routes for spring and autumn migration, a pattern commonly referred to as ‘loop migration’. This pattern has been described using bird ringing data and tracking data based on geolocators in various migratory systems, e.g. *Selasphorus* hummingbirds (Phillips 1975), Marsh Harrier *Circus aeruginosus* (Klaassen *et al.* 2010), Bar-tailed Godwit *Limosa lapponica* (Gill *et al.* 2009), Sand Martin *Riparia riparia* (Szép *et al.* 2017) and Red-backed Shrike *Lanius collurio* (Tøttrup *et al.* 2017).

The size and shape of the migratory loop may differ between populations (Newton 2008). Northern populations typically have longer and more pointed wings than southern populations of the same species (Marchetti *et al.* 1995). Longer, more pointed wings are an adaptation to longer migration distances (e.g. Mönkkönen 1995, Pérez-Tris & Tellería 2001, Arizaga *et al.* 2006, Jaroslaw *et al.* 2014). Based on these findings, loop migration may be detected by the differences in the wing morphology of adult birds between spring and autumn in the same area (Ożarowska *et al.* 2011, Jónás *et al.* 2018).

However, differences in morphology can also be explained by sex, age or moult status, and so these variables have to be controlled. For many songbirds, females and juveniles have been found to be smaller and have shorter wings than adults (Alatalo *et al.* 1984, Tiainen & Hanski 1985, Geen 1988, Bozó & Heim 2016). Moult can also lead to a moderate increase in wing length (in Sylviidae, freshly moulted feathers are 0.4–0.8 mm longer than old ones) (Norman 1997). Species may also differ regarding their moult strategy. There are three common moult strategies among passerines: postnuptial, prenuptial and double moult (Svensson 1992, Jenni & Winkler 2011). For birds with a postnuptial moult (i.e. replacing feathers between the nesting period and the autumn migration), if the average wing length was longer in birds trapped during spring migration at one particular location, loop migration could form a possible explanation. Loop migration may also be

predicted for bird species that are known to moult on the wintering grounds but show a shorter average wing length in spring than in autumn. If these criteria are not met, yet the extent of increase in wing length exceeds the expected growth from moult, loop migration may be suspected (Jónás *et al.* 2018).

Very little is known about the drivers of loop migration, but prevailing winds during migration and/or variation in food availability might play a role (Gauthreaux *et al.* 2006, Shaffer *et al.* 2006, Klaassen *et al.* 2011, Thorup *et al.* 2017, Tøttrup *et al.* 2017). For instance, the wind-assistance hypothesis states that migrants will gain an advantage by migrating over areas that provide greater tailwind assistance or have a weaker headwind. If the dominant wind varies seasonally and regionally, then migrants will use different routes depending on the season, and thus will show loop migration patterns (Arizaga & Tamayo 2013). The dominant wind direction in East and South-East Asia is most commonly easterly or south-easterly during both the spring and autumn migration periods (Dobby 1945, IRI 2019), thus, birds are exposed to similar wind directions in both seasons. The East Asian flyway provides continuous stopover possibilities and lacks major ecological barriers for migrating songbirds (Yong *et al.* 2015), making seasonal detours and loop migration potentially unnecessary. However, a geolocation study found seasonal differences in stopover site locations among Siberian Rubythroats *Calliope calliope*, suggesting a more westerly migration route in autumn (Heim *et al.* 2018a). In a recent study in the Russian Far East, Bozó *et al.* (2018) found a positive effect of tailwind on the numbers of trapped Dusky Warblers *Phylloscopus fuscatus* and Yellow-browed Warblers *P. inornatus* in autumn. In spring, most individuals of these two species were trapped in crosswinds (easterly or westerly winds), which suggested a possible loop migration pattern. However, no effect was found for Pallas’s Leaf Warblers *P. proregulus* and Radde’s Warblers *P. schwarzi*, suggesting that the effect of wind direction might be species-specific.

In this study, we examined differences in wing length among individuals of six passerine species between spring and autumn trapped at two stopover sites in Russia. All of our study species have extremely large distributions in Northern Eurasia and winter

in South-East Asia (Birdlife International 2019). Our study species at both sites are expected to follow the same migratory route along the East Asian coast (Bozó *et al.* 2018), and are unlikely to cross high mountains and deserts (e.g. Himalaya, Altai, Gobi Desert), despite the fact that small numbers of passerines have been found to cross these barriers (Han *et al.* 2007, Delany *et al.* 2017). Based on ecological theory, we expect that the six study species would lack loop migration patterns, and that they would use similar migration routes in both spring and autumn.

MATERIALS AND METHODS

Fieldwork was carried out at two sites in Russia. The first study site is located at Muraviovka Park, along the middle stream of the Amur River in the Russian Far East, 60 km south-east of the city of Blagoveshchensk (49.919°N 127.672°E). Birds were captured with standard mist-nets (Ecotone, Poland) and ringed within the Amur Bird Project (Heim & Smirenski 2013, 2017) during spring (2013, 2015–2017) and autumn (2011–2015, 2017) migration (see Heim *et al.* 2018b). The second study site was located in the buffer zone of the Baikalsky State Nature Biosphere Reserve, which is situated on the south-east coast of Lake Baikal, south-west from the

Mishikha River mouth on the Pribaikalskaya flatland (51.644°N 105.523°E). Surrounding vegetation here is dominated by cedar forests *Cedrus* spp., mixed with birch *Betula* spp., aspen *Populus* spp. and fir *Abies* spp., and alternating with small willow bushes and grass meadows. Birds were captured with Japanese-type mist-nets with a total length of 210 linear metres and ringed within the Baikal Bird Ringing Scheme. Fieldwork here was conducted between 15 April and 20 June in spring and 25 July and 20 October in autumn during 2012–2018.

Data analysis was based on 2,368 captured adult individuals of six species with an appropriate sample size: Red-flanked Bluetail *Tarsiger cyanurus*, Siberian Rubythroat, Taiga Flycatcher *Ficedula albicilla*, Arctic Warbler *Phylloscopus borealis*, Thick-billed Warbler *Arundinax aedon* and Black-faced Bunting *Emberiza spodocephala* (Table 1). Species names and baseline taxonomy follow the IOC World Bird List version 9.2 (Gill & Donsker 2019). Four species (Red-flanked

Table 1. The results of the one-way ANOVA test for differences in wing length between years (MP = Muraviovka Park, LB = Lake Baikal). Significant results are printed in bold font.

| Species | Study site | Season | Sex | df | F | p |
|---|------------|---------------|----------|--------------|---------------|------------------|
| Red-flanked Bluetail <i>Tarsiger cyanurus</i> | MP | autumn | F | 3,23 | 0.542 | 0.658 |
| | MP | autumn | M | 3,32 | 2.179 | 0.110 |
| | LB | spring | M | 2,62 | 0.339 | 0.714 |
| | LB | autumn | M | 2,128 | 0.358 | 0.699 |
| | LB | autumn | F | 1,34 | 2.013 | 0.165 |
| Taiga Flycatcher <i>Ficedula albicilla</i> | MP | spring | M&F | 2,22 | 1.672 | 0.211 |
| | MP | autumn | M&F | 2,18 | 1.548 | 0.239 |
| | LB | spring | M&F | 5,82 | 3.252 | 0.010 |
| | LB | autumn | M&F | 2,25 | 4.428 | 0.022 |
| Arctic Warbler <i>Phylloscopus borealis</i> | MP | spring | M&F | 3,201 | 0.247 | 0.864 |
| | MP | autumn | M&F | 1,25 | 0.051 | 0.823 |
| | LB | spring | M&F | 4,92 | 0.920 | 0.456 |
| | LB | autumn | M&F | 2,13 | 0.173 | 0.843 |
| Black-faced Bunting <i>Emberiza spodocephala</i> | MP | autumn | F | 1,35 | 0.021 | 0.886 |
| | MP | autumn | M | 2,83 | 9.138 | <0.001 |
| | MP | spring | F | 1,18 | 1.822 | 0.194 |
| | MP | spring | M | 1,53 | 0.414 | 0.522 |
| | LB | spring | M | 2,16 | 12.520 | <0.001 |
| | LB | spring | F | 1,15 | 1.835 | 0.196 |
| Thick-billed Warbler <i>Arundinax aedon</i> | LB | autumn | F | 1,15 | 3.550 | 0.080 |
| | MP | spring | M&F | 2,115 | 6.823 | 0.001 |
| | MP | autumn | M&F | 1,17 | 0.593 | 0.452 |
| | LB | spring | M&F | 3,193 | 15.990 | <0.001 |
| Siberian Rubythroat <i>Calliope calliope</i> | MP | spring | M&F | 3,20 | 1.867 | 0.168 |
| | MP | autumn | M&F | 3,72 | 2.101 | 0.110 |
| | LB | spring | M&F | 3,91 | 1.412 | 0.244 |
| | LB | autumn | M&F | 5,89 | 4.267 | 0.010 |

Table 2. The results of the t-tests regarding differences in wing length within seasons (MP = Muraviovka Park, LB = Lake Baikal). Significant results are printed in bold font.

| Species | Study site | Season | Sex | t | p |
|---|------------|---------------|----------|-------------|------------------|
| Red-flanked Bluetail <i>Tarsiger cyanurus</i> | MP | autumn | F | -0.36 | 0.740 |
| | MP | autumn | M | 0.57 | 0.570 |
| | MP | spring | F | 1.59 | 0.130 |
| | MP | spring | M | -0.26 | 0.790 |
| | LB | autumn | F | 0.14 | 0.890 |
| | LB | autumn | M | 0.70 | 0.710 |
| | LB | spring | F | 0.64 | 0.590 |
| | LB | spring | M | 0.06 | 0.950 |
| Taiga Flycatcher <i>Ficedula albicilla</i> | MP | spring | M&F | 0.97 | 0.340 |
| | MP | autumn | M&F | -0.44 | 0.660 |
| | LB | spring | M&F | 3.48 | <0.001 |
| Arctic Warbler <i>Phylloscopus borealis</i> | LB | autumn | M&F | -2.9 | 0.001 |
| | MP | spring | M&F | 1.36 | 0.170 |
| | MP | autumn | M&F | 1.41 | 0.170 |
| Black-faced Bunting <i>Emberiza spodocephala</i> | LB | spring | M&F | 2.90 | 0.004 |
| | LB | autumn | M&F | 1.96 | 0.060 |
| | MP | spring | F | 1.10 | 0.350 |
| | MP | spring | M | 1.30 | 0.190 |
| Thick-billed Warbler <i>Arundinax aedon</i> | MP | autumn | F | -0.22 | 0.840 |
| | MP | autumn | M | -2.5 | 0.010 |
| | LB | spring | F | 0.76 | 0.460 |
| | LB | spring | M | 0.72 | 0.480 |
| | LB | autumn | F | -1.24 | 0.240 |
| | LB | autumn | M | -1.61 | 0.160 |
| Siberian Rubythroat <i>Calliope calliope</i> | MP | spring | M&F | 3.17 | 0.001 |
| | MP | autumn | M&F | 0.77 | 0.760 |
| | LB | spring | M&F | 0.57 | 0.570 |
| | LB | autumn | M&F | 0.19 | 0.190 |
| Siberian Rubythroat <i>Calliope calliope</i> | MP | spring | M&F | 0.13 | 0.930 |
| | MP | autumn | M&F | 0.05 | 0.960 |
| | LB | spring | M&F | 4.77 | <0.001 |
| Siberian Rubythroat <i>Calliope calliope</i> | LB | autumn | M&F | -0.66 | 0.510 |

Bluetail, Siberian Rubythroat, Taiga Flycatcher and Black-faced Bunting) show pronounced sexual dimorphism; however, due to the small sample sizes, only the males and females of Red-flanked Bluetail and Black-faced Bunting were analysed separately (Table 1). For both species, we also checked the rate of trapped males and females in both seasons at both study sites (Table 2).

The species, sex and age of the captured individuals were identified using Svensson (1992), Brazil (2009) and Demongin (2016). From the recorded biometric data only the wing length was used for this study, and this was measured by the 'maximum flattened chord method' (Svensson 1992) to the nearest mm. Considering the variability in measurements caused by different bird-ringers, we compared the wing length measurements of all ringers for both study sites. We included only data of ringers whose measurements do not differ significantly from the reference person. The reference person was the second author in the case of birds ringed and measured at Muraviovka Park, and the third author for birds ringed at Lake Baikal, based on the most ringed and measured individuals of all species.

We tested for wing length differences within the seasons, since within-season patterns may influence the variation of wing morphology at a stopover site (Chernetsov 2004). We divided the migration seasons into a first and a second part for all study species and the wing length values of the two parts were compared using a two-sample t-test. In addition, we also tested the possible differences in the wing length values among years using a one-way ANOVA. General linear models (GLMs) were used to evaluate the possible factors affecting wing lengths patterns. The following independent variables were tested to explain the dependent variable wing length: sex, season progress (Julian date) and year of the study.

Four out of the six study species (Red-flanked Bluetail, Siberian Rubythroat, Taiga Flycatcher and Black-faced Bunting) exhibit postnuptial moults while the other two species (Arctic Warbler and Thick-billed Warbler) exhibit prenuptial moults (Svensson 1992). We compared average autumn and spring wing length values using Welch's t-test (Reiczigel *et al.* 2014) (Table 3). All statistical analyses were carried out using R 3.2.4 (R Core Team 2016).

RESULTS

Differences in wing length values between years and within seasons

Significant differences in wing length values between years were found for Taiga Flycatcher (at Lake Baikal in both seasons), Black-faced Buntings (males in spring at Lake Baikal and in autumn at Muraviovka Park), Thick-billed Warbler (in spring at both study sites) and Siberian Rubythroat (in autumn at Lake Baikal) (Table 1).

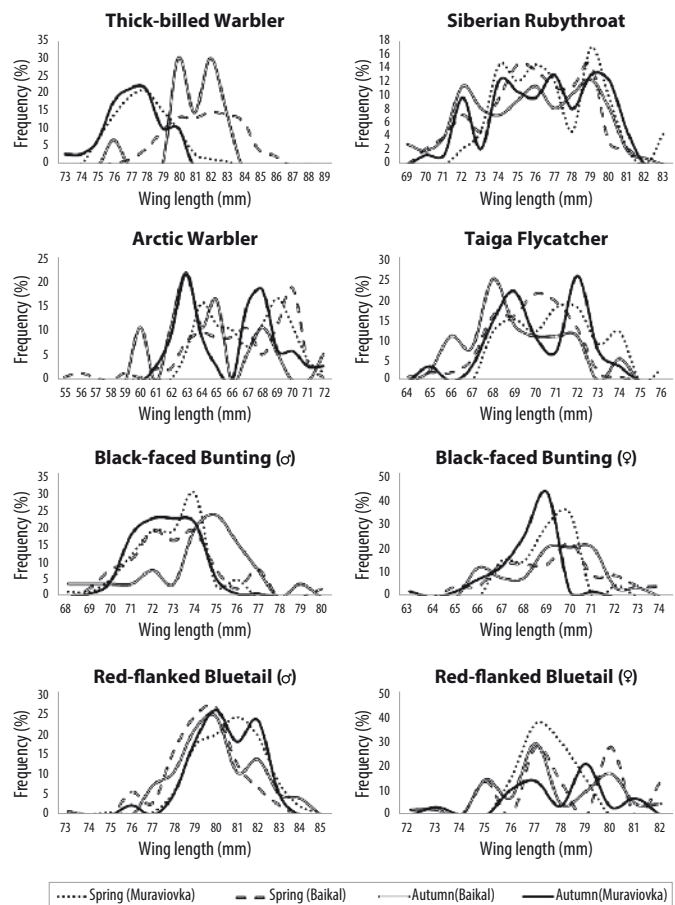
We found a significant decrease in wing length during the progress of spring migration for Taiga Flycatcher (Lake Baikal), Thick-billed Warbler (Muraviovka Park) and Siberian Rubythroat (Lake Baikal). A significant increase in wing length was found in autumn for Taiga Flycatcher (Lake Baikal) and Black-faced Bunting (Muraviovka Park) (Table 2).

Species performing a postnuptial moult

Significant differences in wing length measured in spring and autumn were found for female Black-faced Buntings at Muraviovka Park and for male Red-flanked Bluetails at Lake Baikal, as well as for Red-flanked Bluetails of both sexes combined at Muraviovka Park (Table 1).

The distribution of wing lengths measured in spring and autumn overlapped at both study sites in Siberian Rubythroat and Taiga Flycatcher (Figure 1). The same pattern was found for males and females of Red-flanked Bluetails at Lake Baikal and females at Muraviovka Park, and male Black-faced Buntings at Muraviovka

Figure 1. Wing lengths of the six study species in spring and autumn at the two study sites.



Park and females at Lake Baikal (Figure 1). However, the proportion of longer-winged Red-flanked Bluetail females at Muraviovka Park and male Black-faced Buntings at Lake Baikal was greater in autumn, while the proportion of longer-winged Black-faced Bunting females was greater in spring at Muraviovka Park.

The ratio between trapped males and females did not differ in Black-faced Buntings, while in the case of Red-flanked Bluetail more males were trapped in spring than in autumn at both study sites, which explains the longer wing length of birds in spring, if we treat both sexes together (Table 2).

Species performing a prenuptial moult

No significant differences in wing length between seasons were found for Arctic and Thick-billed Warblers (Table 1). However, the distribution of spring and autumn wing length measurements of both species overlapped, although in the case of the Arctic Warbler the proportion of shorter-winged birds was greater in autumn at both study sites (Figure 1).

Factors affecting wing length values

The only factor significantly affecting wing length values was the sex in Black-faced Buntings at both study sites and in Siberian Rubythroats at Muraviovka Park (Table 4).

DISCUSSION

We found no differences in wing length between spring and autumn migration for most of the study species, suggesting the absence of loop migration. This may be because of 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

Table 3. Mean wing lengths, differences between spring and autumn mean wing lengths (Diff.) and the results of the statistical analyses (Welch's t-test). SD = standard deviation, df = degree(s) of freedom, MP = Muraviovka Park and LB = Lake Baikal. Wing length values and differences are given in mm. Significant p-values are indicated by bold numbers.

| Species | Sex | Study site | Sample size | | Wing length (mean) | | Wing length (SD) | | Diff. | p-value | t-value | df |
|---|-----|------------|-------------|--------|--------------------|--------|------------------|--------|-------|---------------|---------|-----|
| | | | Spring | Autumn | Spring | Autumn | Spring | Autumn | | | | |
| Black-faced Bunting <i>Emberiza spodocephala</i> | M | MP | 56 | 87 | 72.6 | 72.4 | 1.7 | 1.5 | -0.2 | 0.5093 | 0.6622 | 104 |
| | | LB | 36 | 26 | 73.6 | 73.2 | 2.3 | 3.5 | -0.4 | 0.5936 | 0.5380 | 40 |
| | F | MP | 20 | 39 | 68.8 | 67.8 | 1.3 | 1.4 | -1.0 | 0.0079 | 2.7962 | 40 |
| | | LB | 22 | 24 | 69.6 | 69.3 | 3.0 | 1.9 | -0.3 | 0.6476 | 0.4611 | 35 |
| | M&F | MP | 76 | 134 | 71.8 | 71.1 | 2.6 | 2.3 | -0.7 | 0.0575 | 1.9127 | 170 |
| | M&F | LB | 96 | 55 | 71.3 | 71.6 | 3.0 | 3.5 | 0.3 | 0.6250 | 0.4904 | 98 |
| Red-flanked Bluetail <i>Tarsiger cyanurus</i> | M | MP | 138 | 38 | 80.4 | 80.1 | 1.6 | 1.6 | -0.3 | 0.2660 | 1.1229 | 59 |
| | | LB | 186 | 93 | 79.4 | 80.0 | 1.7 | 1.9 | 0.6 | 0.0140 | 2.4839 | 160 |
| | F | MP | 13 | 28 | 77.3 | 77.7 | 0.9 | 1.5 | 0.4 | 0.2513 | 1.1666 | 35 |
| | | LB | 7 | 40 | 78.4 | 77.6 | 2.4 | 2.4 | -0.8 | 0.4314 | 0.8285 | 8 |
| | M&F | MP | 152 | 69 | 80.4 | 79.3 | 1.8 | 2.0 | -1.1 | 0.0003 | 3.7431 | 118 |
| | M&F | LB | 215 | 151 | 79.3 | 79.1 | 1.8 | 2.4 | -0.2 | 0.5975 | 0.5286 | 260 |
| Siberian Rubythroat <i>Calliope calliope</i> | M&F | MP | 41 | 122 | 76.9 | 76.4 | 2.7 | 2.9 | -0.5 | 0.3141 | 1.0138 | 72 |
| | | LB | 123 | 96 | 75.9 | 75.7 | 2.7 | 3.2 | -0.2 | 0.5604 | 0.5833 | 184 |
| Taiga Flycatcher <i>Ficedula albicilla</i> | M&F | MP | 27 | 33 | 70.2 | 71.1 | 2.1 | 2.1 | 0.9 | 0.0916 | 1.7170 | 55 |
| | | LB | 93 | 36 | 69.7 | 69.1 | 1.9 | 2.3 | -0.6 | 0.1829 | 1.3493 | 54 |
| Thick-billed Warbler <i>Arundinax aedon</i> | M&F | MP | 129 | 27 | 77.9 | 77.2 | 1.8 | 1.8 | 0.7 | 0.0637 | 1.9103 | 38 |
| | | LB | 305 | 13 | 81.6 | 80.6 | 2.4 | 2.1 | 1.0 | 0.1062 | 1.7362 | 13 |
| Arctic Warbler <i>Phylloscopus borealis</i> | M&F | MP | 205 | 32 | 66.9 | 65.9 | 2.6 | 3.1 | 1.0 | 0.0878 | 1.7522 | 38 |
| | | LB | 110 | 18 | 66.3 | 64.6 | 3.6 | 3.2 | 1.7 | 0.0581 | 1.9904 | 24 |

Table 4. Sex ratios of captured Black-faced Buntings and Red-flanked Bluetails in spring and autumn.

| Species | Ratio (M) | | | | Ratio (F) | | | |
|---|------------|--------|--------|--------|------------|--------|--------|--------|
| | Muraviovka | | Baikal | | Muraviovka | | Baikal | |
| | Spring | Autumn | Spring | Autumn | Spring | Autumn | Spring | Autumn |
| Black-faced Bunting <i>Emberiza spodocephala</i> | 0.74 | 0.69 | 0.62 | 0.52 | 0.26 | 0.31 | 0.38 | 0.48 |
| Red-flanked Bluetail <i>Tarsiger cyanurus</i> | 0.91 | 0.58 | 0.96 | 0.70 | 0.09 | 0.42 | 0.04 | 0.30 |

to be crossed during migration along the East Asian flyway. However, these general findings do not necessarily apply to all species, and for some, the results obtained are inconsistent with previous studies.

We found significant differences in wing length between years for some of our study species. All of the studied species moult their flight feathers annually, and moult is costly in terms of energy (Lindström *et al.* 1993). If weather conditions are unfavourable (e.g. drought or too much rainfall), 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, Jenni & Winkler 1989). The analyses of long-term datasets have shown that wing length can vary significantly between years, most likely for the above-mentioned reason. Such a pattern was suggested for several widespread species in Europe, e.g. Dunnock *Prunella modularis* (Harnos *et al.* 2016a), Common Nightingale *Luscinia megarhynchos* (Csörgő *et al.* 2017a), Thrush Nightingale *L. luscinia* (Csörgő *et al.* 2018), Common Blackbird *Turdus merula* (Csörgő *et al.* 2017b), Song Thrush *T. philomelos* (Csörgő *et al.*

2017c) and Pied Flycatcher *Ficedula hypoleuca* (Harnos *et al.* 2016b).

Wing length frequency distributions often show substantial deviation from the normal distribution, and there are several peaks of wing lengths. This could be explained by the occurrence of several populations with distinct wing biometry at the same sampling site, or to sex-specific migration timing. Our models revealed sex as the only factor determining wing length, and we found no evidence for different populations migrating through the area. Decreased wing length of birds sampled in spring most likely reflects protandrous migration, i.e. males (with longer wings) migrate ahead of females to reach the breeding grounds earlier (Durman 1967, Lawn 1974, Reynolds 1978, Boz & Heim 2016). The increased wing length of birds sampled in autumn may also be explained by sex-specific migration. This pattern could be caused by intraspecific competition (males singing during autumn; Logan & Hyatt 1991, Weggler 2000) or by males seeking new nesting sites for the next breeding season (Forstmeier 2002, Mills 2005). If the observed

pattern has been caused by different populations migrating through our study sites, we would expect the opposite pattern: northernmost breeding populations are most likely longer-winged than southern populations (Marchetti *et al.* 1995), and they ought to migrate through the area earlier in spring and later in the autumn.

For Siberian Rubythroats, Weng *et al.* (2014) used stable isotopes and found that birds wintering in Taiwan originate from the southern part of the species's breeding range, which indicates that Siberian Rubythroat exhibits a leapfrog migration. Using geolocators, Heim *et al.* (2018a) found that the birds seem to follow rather straight paths without major detours towards their final winter destinations. These birds initiated migration in autumn by moving westward, far from the shore. This was the first study describing seasonally different stopover sites used by this species, but there was no indication for loop migration. Our study confirms these findings by finding no seasonal difference in wing length at both study sites.

The migration ecology of the Red-breasted Flycatcher *F. parva*, a species closely related to the Taiga Flycatcher (Li & Zhang 2004, Svensson *et al.* 2005), is well studied (e.g. Byshnev & Stavrovsky 1998, Mitrus *et al.* 2005, Mitrus 2007, del Hoyo *et al.* 2019). In spite of the common occurrence of loop migration among European *Ficedula* and *Muscicapa* flycatchers, this pattern has not been described in these two sister taxa (Pilaastro *et al.* 1998, Harnos *et al.* 2015a, Briedis *et al.* 2016, Jónás *et al.* 2018, Taylor & Christie 2019), which is in accordance with our findings.

In the Black-faced Bunting, wing lengths did not differ significantly between birds sampled during spring and autumn migration. Our results suggest that males of this species are unlikely to exhibit loop migration. In contrast, the wing lengths of females differed significantly between spring and autumn seasons at Muraviovka Park, which indicates that females could possibly undertake loop migration. This is an interesting finding, because in passerines with sex-dependent loop migration, the males are generally more likely to undertake loop migration to shorten their routes back to the breeding area in spring, while females use the same route in both seasons (Newton 2008, Harnos *et al.* 2015a,b). Our finding may suggest differential migration patterns for this species during spring and autumn. There are very few examples for bunting species undertaking loop migration, but see, for instance, the Ortolan Bunting *Emberiza hortulana* (Stolt 1977, Yosef & Tryjanowski 2002), which has an extremely broad distribution across Eurasia (Birdlife International 2019). Further studies of the migration ecology of the Black-faced Bunting should consider a larger sample size and include tracking work, for example with geolocators, to support or refute its alleged loop migration pattern.

While several studies have investigated the migration of Red-flanked Bluetail (Gao & Li 1983, Komeda & Ueki 2002, Wang *et al.* 2006), loop migration has not been described previously. Some closely related European species, such as the Common Redstart *Phoenicurus phoenicurus* (Kristensen *et al.* 2013), Northern Wheatear *Oenanthe oenanthe* (Schmaljohann *et al.* 2012a, b), Thrush Nightingale (Kováts 2012, Csörgő *et al.* 2018, Klvaňa *et al.* 2018), Common Nightingale (Csörgő *et al.* 2017a, Jónás *et al.* 2018) and Bluethroat *Luscinia svecica* (Arizaga & Tamayo 2013), are known to exhibit loop migration. In our study, if we treated males and females together, the wing lengths of sampled Red-flanked Bluetail individuals differ significantly between spring and autumn seasons at Muraviovka Park, while at Lake Baikal, only males have significantly longer wings in autumn than in spring. Based on the ratio between captured males and females in spring and autumn, we can conclude that the proportion of adult males was much higher in spring than autumn at both sites. Therefore, the significantly longer wing length in spring compared to autumn is likely driven by the higher proportion of males, since males have longer wings than females (Svensson 1992). However, in the case of males sampled at Lake Baikal—with an appropriate sample size—the significant difference in wing length may reflect loop migration.

A recaptured bird adds further support to this possibility: a Red-flanked Bluetail ringed on 21 April 2015 during spring migration at Muraviovka Park was recaptured on 8 October 2015 during autumn migration at Lake Baikal (Y. Anisimov, W. Heim, unpubl. data). This male might have taken a more easterly route during spring migration. In spring, males are presumed to migrate faster than females in many European (Durman 1967, Lawn 1974, Reynolds 1978, Coppack *et al.* 2006) and Siberian (Bozó & Heim 2016) species. This phenomenon results in males which cross instead of avoid ecological barriers in spring performing a loop migration (Newton 2008). There is evidence that some species, including passerines, are able to fly through high mountains, even the Himalaya (Delany *et al.* 2017). This hypothesis might be true for the Red-flanked Bluetail, as potential barriers, especially higher mountain ranges in the Lake Baikal area, are situated to the west of Muraviovka Park. The recapture mentioned above may confirm this hypothesis, and this may also indicate that birds migrating through the study area in autumn originated from more westerly breeding areas.

Long-distance migrant European *Phylloscopus* species such as the Wood Warbler *P. sibilatrix* (Wernham *et al.* 2002) and Willow Warbler *P. trochilus* (Pearson & Lack 1992, Jónás *et al.* 2018) are known to show a loop migration pattern. However, we could not find such a pattern among Arctic Warblers at our study sites. The differences between wing lengths measured in the spring and autumn were insignificant even though measured wing lengths of birds sampled were 1.0 and 1.7 mm shorter in autumn than in spring at both sites. The current evidence for loop migration for the Arctic Warbler is anecdotal, but may benefit from increased sampling efforts.

There is limited information on the migration of Thick-billed Warbler (Malyshev 1960, Neufeldt 1967, Dementiev & Gladkov 1968, Williams 2000, Bozó *et al.* 2016), and these studies, as well as Dyrz (2019), do not mention the species as being a loop migrant. Our results provide broad support for this, despite the fact that some closely related species, such as Savi's Warbler *Locustella luscinioides* (Jónás *et al.* 2018) and Great Reed Warbler *Acrocephalus arundinaceus* (Horns *et al.* 2016, Koleček *et al.* 2016), exhibit loop migration.

It is worth mentioning, however, that the lack of significant differences in wing lengths of migrating passerines sampled between the seasons does not necessarily demonstrate the absence of loop migration. This is because such differences might have arisen due to low natural variation in wing lengths or be the result of latitudinal migration directions of the species, as was assumed by Johansen (1954) for Arctic Warblers. However, latitudinal migration is not yet proved for any of the study species with recapture data or geolocators. Most Siberian passerines may avoid large barriers such as the Himalaya and Gobi Desert on migration, and use a longer and more easterly migration route (e.g. McClure 1974). However, there are some species that do cross these mountains and deserts during their migration (Delany *et al.* 2017). Furthermore, the studied species have extremely large distribution ranges (Birdlife International 2019) without known significant variation in their biometrics (del Hoyo *et al.* 2006). Therefore, while differences in wing lengths are indicative of loop migration, they are not necessarily sufficient on their own to demonstrate loop migration patterns.

Put together, our existing findings provide preliminary evidence for loop migration in two Siberian-breeding migratory passerines, but not for four other species sampled. A major limitation in our study is our small sample sizes, which highlights the importance of continuing sampling of these species in the future to fill current data gaps, across different study sites. In recent years, the populations of some East Asian species have declined due to illegal trade, hunting and habitat loss (Kamp *et al.* 2015, Yong *et al.* 2015, Edenius *et al.* 2017). To be able to take appropriate steps to protect these species, basic research on the migration ecology of more migratory passerines in the East Asian flyway should be strengthened, and scaled across a broad geographical range in the region.

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