



# Factors controlling the migration phenology of Siberian *Phylloscopus* species

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## Abstract

The timing of annual events in migratory species is determined by the position of breeding and wintering grounds, length of the breeding season, the occurrence of their preferred diet or the timing of moult in birds. Previous studies found significant differences in the migration phenology of Asian *Phylloscopus* warbler species, a group of long-distance migratory passerines. However, the factors that influence the observed differences in migration phenology have not been studied yet. Here, we analyze the effect of the above-mentioned factors on the migration timing of seven *Phylloscopus* species at a stopover site in the Russian Far East. We found that spring migration phenology was best explained by moult strategy and the preferred prey size, while autumn migration phenology was linked to the southernmost wintering latitude of the species. Interspecific differences in migration timing were much higher in autumn than in spring. The duration of the species-specific migration periods was also longer in autumn than in spring, most likely caused by higher competition during spring to arrive early at the breeding grounds. Our results contribute to the understanding of migration ecology in songbirds moving along the little-studied East Asian flyway.

**Keywords** Leaf warbler · Migration strategies · East Asian flyway · Diet

## Zusammenfassung

### Welche Faktoren bestimmen die Zugphänologie sibirischer Laubsänger?

Der Jahreszyklus ziehender Arten wird von der Lage der Brut- und Überwinterungsgebiete, der Länge der Brutsaison, der Verfügbarkeit bevorzugter Nahrung oder dem Zeitraum der Mauser bestimmt. Vorhergehende Studien fanden signifikante Unterschiede in der Zugphänologie von asiatischen Laubsängern, einer Gruppe von Langstreckenziehern. Die Ursachen für die beobachteten Unterschiede wurden bisher jedoch noch nicht untersucht. Hier analysieren wir den Einfluss der oben genannten Faktoren auf das zeitliche Auftreten von sieben Laubsänger-Arten an einem Zwischenrastplatz im Fernen Osten Russlands. Im Frühjahr konnten die Unterschiede in der Phänologie der Arten am besten mit der Mauserstrategie und der Größe der bevorzugten Nahrung erklärt werden, während die Phänologie des Herbstzuges mit dem südlichsten Breitengrad des Überwinterungsgebietes erklärt werden konnte. Die zeitlichen Unterschiede zwischen den Arten waren im Herbst größer als während des Frühjahrszuges. Die artspezifischen Zugperioden waren im Herbst ebenfalls länger als im Frühjahr. Dies kann mit der Konkurrenz um ein möglichst zeitiges Ankommen in den Brutgebieten erklärt werden. Unsere Ergebnisse tragen zu einem besseren Verständnis der Zugökologie von Singvögeln des wenig untersuchten ostasiatischen Zugweges bei.

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## Introduction

Migratory birds connect continents and different bioms during their long journey twice each year (Hahn et al. 2009). An estimated four billion migratory birds, the majority of which are passerines, migrate annually from temperate Eurasia to lower latitudes in Africa and Asia during the boreal winter (Newton 2007).

The phenology of migration relates to repeating cycles of life-history stages, such as migration, moult and breeding (Piersma and Ramenofsky 1998; Piersma and Drent 2003). Moult is costly in terms of energy (Lindström et al. 1993), and there is a strong correlation between the termination of moult and the onset of migration (Pulido and Coppack 2004). Therefore, moult strategy is a key regulator of the autumn migration. Among Palaearctic migratory songbirds, about half of the long-distance migrants moult directly after breeding (postnuptial moult) while the other half moult on the wintering grounds (prenuptial moult) (Barta et al. 2008). The different moult strategies appear to depend on the distance between the breeding and wintering grounds (Ginn and Melville 1983; Jenni and Winkler 2020). Phylogenetical analyses of moult strategies of warblers indicated, that species with longer migration routes tend to moult on the wintering grounds (Svensson and Hedenström 1999).

Another important factor for differences in phenology is the migration distance a species has to cover between breeding and wintering grounds (Marchetti et al. 1995). Species with long migration distances tend to migrate earlier in autumn and later in spring compared to short-distance migrants (Jenni and Kéry 2003).

Besides moult and migration distance, wintering behaviour shapes migration and breeding phenology (Marra et al. 1998). Conditions during winter also affect arrival schedules and the birds' condition in the breeding season, as well as the birds' reproductive success (Verboven and Visser 1998; Marra et al. 1998). The relationship between arrival date on the breeding grounds and the expected reproductive success can strongly influence the migratory behavior of individuals (Weber et al. 1998, 1999). In American Redstarts (*Setophaga ruticilla*), birds wintering in higher-quality habitats were found to depart earlier from the wintering grounds because of their better body conditions (Marra and Holberton 1998; Marra et al. 1998; Studds and Marra 2005). Furthermore, the timing of the onset of autumn migration also depends on the number of broods (Jenni and Kéry 2003) and the length of the breeding season (Ellegren 1990; Fransson 1995).

On top of that, migration phenology might be shaped by the availability of the preferred prey. Katti and Price (2003) found that the size of the preferred prey shapes the distribution of leaf warblers in breeding and wintering grounds in India: smaller species would return earlier to the breeding

grounds than larger taxa because their smaller prey becomes available sooner.

Despite the fact that the East Asian migratory flyway is the largest of all other flyways and holds the highest diversity of migratory songbirds, we have only very limited information about the migration ecology and phenology for most of the species (Yong et al. 2015). Short-term but standardized bird-ringing activities have resulted in a better understanding of feeding habits, habitat use, and migration strategies in several groups of Asian passerines, for example small thrushes (Wang et al. 2006; Maslovsky et al. 2018), and buntings (Nam et al. 2011; Heim et al. 2018). However, in the last two decades the most studied group in Asia were the leaf warblers. We have detailed information on breeding ecology (e.g., Price and Jamdar 1991; Bourski and Forstmeier 2000; Forstmeier et al. 2001a; Forstmeier 2002; Forstmeier and Balsby 2002), habitat use, morphology and foraging strategies (Price 1991; Forstmeier et al. 2001b; Katti and Price 2003; Batova 2011; Bozó et al. 2018a), the sex-specific timing of migration (Bozó and Heim 2016), the effect of weather variables on the migration (Bozó et al. 2018b) and the estimated migration distances (Sander et al. 2017; Bozó et al. 2019) of these species. However, the factors that influence the observed differences in migration phenology have not been studied yet.

In this study, we investigated factors possibly shaping the migration phenology of a set of leaf warbler species at a stop-over site in the Russian Far East. Since the timing of moult determines the migration timing of birds, we assume that (1) species with a postnuptial moult strategy start their migration later in autumn than species exhibiting prenuptial moult. We also tested (2) the effect of the geographical position of species-specific wintering grounds on the migration phenology. We hypothesize that (3) breeding biology influences the migration timing of the study species: species with an early breeding season would migrate earlier in autumn than species with a late breeding season (cf. Jenni and Kéry 2003). Furthermore, we test (4) whether the size of the preferred prey would explain the observed migration phenology.

## Material and methods

The study was carried out within the Amur Bird Project (Heim and Smirenski 2013, 2017) at Muraviovka Park along the middle reaches of the Amur River in the Russian Far East. The study site is located 60 km southeast of the city of Blagoveshchensk (49°55'08,27"N, 127°40'19,93"E). Birds were trapped with mist-nets using a constant-effort-site approach in a variety of different habitat types (for details see Heim et al. 2018). We included the following species: Yellow-browed Warbler *Phylloscopus inornatus*, Arctic Warbler *P. borealis*, Two-barred Warbler *P. plumbeitarsus*,

Pale-legged Leaf Warbler *P. tenellipes*, Dusky Warbler *P. fuscatus*, Radde's Warbler *P. schwarzi* and Pallas's Leaf Warbler *P. proregulus*. A total of 9211 trapped individuals of all species combined were available for analysis (Table 1).

Two of the study species, Dusky Warbler and Pale-legged Leaf Warbler, are not only migrants but breed at the study site (Heim 2014). Therefore, mainly in case of the more common Dusky Warbler, it is not possible to separate local and transient individuals, and the median day of occurrence might be biased by local breeding birds. However, both species start to breed from late May-early June and finish breeding in late July in Southeast Russia (Clement 2006a, b), so we assume that the overlap between migration and breeding periods are negligible. Furthermore, the overall number of possible breeders is very small compared to the large numbers of migrating individuals. In addition, we excluded all individuals that were recaptured during the breeding season.

For the analysis of phenology, we included birds captured in mist-nets during spring (25th April to 10th June in 2013, 2015–2017) and autumn (1st August to 20th October in 2013, 2014, 2015 and 2017) migration. We defined the length of the species-specific migration periods as the number of days between the first and the last capture.

We used Kruskal–Wallis tests to analyze differences in the timing of migration between the study species, and paired *t* tests for differences between the length of spring and autumn migration period. To test the impact of different variables on migration timing, we used generalized linear mixed-effect models (GLMMs) within the R package lme4 (Bates et al. 2007). The following factors were used to explain the dependent variable *migration day* for spring and autumn: southernmost wintering latitude, end of the breeding period, moulting strategy (pre-nuptial or post-nuptial) and the average size of the prey. The selected fixed factors were not strongly correlated ( $R < 0.5$ ). *Species* and *year* were fitted as random factors. Significant variables were selected with the help of “backward stepwise model selection”

(Crawley 2013) using the Likelihood-ratio test ( $p < 0.05$ ). Information about the distribution of the study species was gathered from the IUCN range maps (BirdLife International 2019). Data regarding diet and breeding were taken from the following sources: Price (1991); Glutz von Blotzheim and Bauer (1991); Forstmeier and Kessler (2001); Forstmeier et al. (2001b); Katti and Price (2003); del Hoyo et al. (2006); Batova (2011). The average timing of the beginning and end of the nesting period was gathered from the literature for the entire breeding area, as very few data are available from different geographical regions. Mean prey size was calculated by the typical size of the prey based on information from the literature. In many cases, only higher taxa and groups were specified, so these prey sizes represent rough estimates (see supplementary material 2). No detailed information on diet was available for the Pale-legged Leaf Warbler, but based on descriptions in the literature we estimated the average prey size at 10 mm. Two of the seven study species (Arctic Warbler and Two-barred Warbler) have complete pre-nuptial moult, while the other species have complete post-nuptial moult (Svensson 1992; Brazil 2009; Demongin 2016). All data are given in Table 2.

All statistical analyses were carried out using the program R version 3.6.2 (R Core Team 2019).

## Results

We found significant differences in the timing of migration among the seven studied leaf warbler species both in spring (Kruskal–Wallis test,  $H = 1151$ ,  $p < 0.0001$ ) and in autumn (Kruskal–Wallis test,  $H = 1202$ ,  $p < 0.0001$ ) (Fig. 1). Spring migration begins with Pallas's Leaf Warbler and Yellow-browed Warbler as the earliest species to arrive at the study site. The species migrating last are Two-barred Warbler and Arctic Warbler. Autumn migration starts in early August for

**Table 1** The number of trapped individuals, the median migration dates and the length of the migration periods of the seven study species

Species	Spring		Autumn		Median date		Length of migration period (days)	
	Standard	Non-standard	Standard	Non-standard	Spring	Autumn	Spring	Autumn
<i>P. inornatus</i>	2048	338	1718	603	14 May	7 Sep	116	158
<i>P. borealis</i>	202	38	183	47	27 May	23 Aug	138	160
<i>P. plumbeitarsus</i>	57	8	114	33	31 May	27 Aug	139	161
<i>P. tenellipes</i>	30	11	146	45	19 May	15 Aug	137	158
<i>P. fuscatus</i>	749	154	1328	522	21 May	7 Sep	119	160
<i>P. schwarzi</i>	96	7	191	62	25 May	11 Sep	129	161
<i>P. proregulus</i>	72	11	276	122	22 May	25 Sep	119	157

Numbers are shown separately for birds trapped in standard mist-nets (used in all study years) and for birds trapped in non-standard nets (not used in all study years)

**Table 2** Potential factors shaping the migration phenology of East Asian warbler species, including data on distribution, migration distance, breeding biology and diet, start and end of breeding = number of decades from 1st May to 31 August (1–12)

Variable	<i>inornatus</i>	<i>borealis</i>	<i>plumbeitarsus</i>	<i>proregulus</i>	<i>fuscatus</i>	<i>schwarzi</i>	<i>tenellipes</i>
Northernmost breeding latitude	70	72	62	61	66	58	54
Southernmost breeding latitude	40	42	41	43	28	38	37
Northernmost wintering latitude	27	18	24	32	33	23	22
Southernmost wintering latitude	2	– 11	9	18	2	8	3
Migration distance (°latitudes)	40.5	53.5	35	27	29.5	32.5	33
Number of broods	1	1	1	2	1	1	1
Start of breeding	4	4	3	4	3	4	3
End of breeding	10	9	11	9	11	10	9
Clutch size	3	6	6	5	5	4	5
Incubation + nestling phase (days)	25	26	26	26	26	27	22
Winter moult	0	1	1	0	0	0	0
Average prey size (mm)	5.4	10	5.6	5.3	11.8	20.6	10

Furthermore, the moult strategy for the studied species is given (0 = complete summer moult, 1 = complete winter moult)

Pale-legged Leaf Warblers and Arctic Warblers and ends in late September and early October with Pallas's Leaf Warbler as the latest migrating species (Fig. 1). The duration of spring migration was significantly shorter than autumn migration ( $t = -3.585$ ,  $p = 0.004$ ).

Our GLMMs revealed that autumn migration phenology is explained best by the southernmost wintering latitude, while spring migration phenology was explained by moult strategy and prey size (Table 3, supplementary material 1).

## Discussion

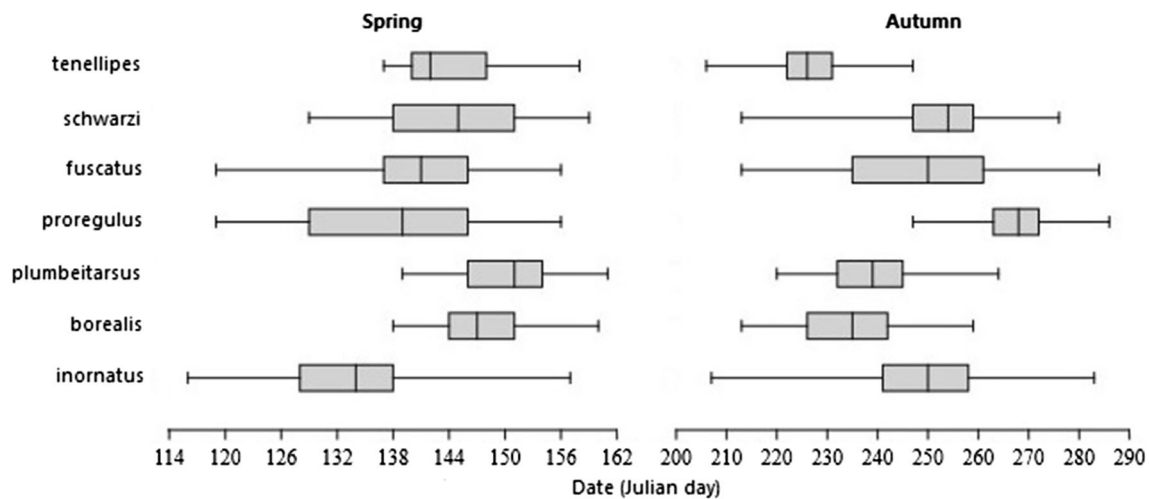
We found significant differences in the migration phenology among a set of East Asian *Phylloscopus* species. Their migration phenology at the study site was found to be related to moult and the size of their preferred prey in spring, and the position of their southernmost wintering areas in autumn.

While most studies found an effect of moult on the timing of autumn migration (Owen and Krohn 1973; Kjellén 1994; Pérez-Tris et al. 2001; Pulido and Coppack 2004), we found that spring migration was related to moult strategy in our study species. In migratory birds, there is a strong correlation between the termination of moult and the onset of migration (Pulido and Coppack 2004). Summer moult occurs when food has a high peak after breeding, while winter moult occurs if there is a short period of high food availability in summer and a strong winter peak at different locations (Barta et al. 2008). Long-distance migrant species usually moult their flight feathers in the wintering grounds (in the beginning or in the end of the winter season; Salewski et al. 2004), or at stopover sites, including some *Locustella* and *Acrocephalus* species (Hedenström et al. 1993; Neto et al. 2006), as in the short Palearctic summer they have no time left between breeding and the preparation for migration (Barta et al. 2008). As moulting is costly in terms of

**Table 3** Effects of southernmost wintering latitude, end of the breeding season, moult strategy and average prey size on the migration phenology of seven warbler species in spring and autumn

Dependent variable	Independent variable	Chi square	$p$	$R^2$ marg	$R^2$ cond
Median migr. day (spring)				0.114	0.139
	Southernmost wintering latitude	2.802	0.094		
	End of breeding	0.127	0.721		
	Moult	<b>9.631</b>	<b>0.002</b>		
Median migr. day (autumn)	Average prey size (mm)	<b>5.182</b>	<b>0.023</b>		
				0.085	0.302
	Southernmost wintering latitude	<b>3.907</b>	<b>0.048</b>		
	End of breeding	0.030	0.862		
	Moult	0.571	0.450		
	Average prey size (mm)	0.002	0.968		

Year and species were fitted as random factors. Categories of variables are the same defined in Table 2. Shown are Chi square,  $p$  value as well as marginal and conditional  $R^2$  of GLMMs



**Fig. 1** Migration phenology of the seven studied warbler species during spring and autumn. The date is given as the number of the day of the year (114 = 23th April, 162 = 10th June, 200 = 18th July, 290 = 16th October)

energy (Lindström et al. 1993), a pre-breeding moult would negatively affect preparation for migration in species that have to migrate longer distances. Spring migration might be delayed in species moulting in winter, as species replacing flight feathers during winter may delay departure compared to species that moult in summer (Rubolini et al. 2005). This could be the case for Arctic and Two-barred Warblers in our study.

Furthermore, we found an interesting relationship between spring migration phenology and mean prey size. Prey size and abundance have been found to be the main determinants of the spring arrival time of *Phylloscopus* warblers in India as well (Katti and Price 2003). In general, larger-bodied animals are typically able to handle larger prey (McNab 1971), which is true for *Phylloscopus* warblers as well (Price 1991; Gross and Price 2000). In boreal forests, the number of insects related to coniferous trees is much higher than those related to deciduous trees, and insects on coniferous trees appear much earlier than on deciduous trees, as the latter develop leaves later in the spring (Southwood 1961). In the temperate zone, therefore, several species of Passerines (tits, Goldcrests *Regulus regulus*) overwinter in pines, as small insects are available there even in winter (Haraszthy 1998; del Hoyo et al. 2006). The smallest and most typical taiga species (Pallas's Leaf Warbler, Yellow-browed Warbler) migrated earlier in spring than the other species in our study, probably because their small prey becomes available earlier.

Autumn migration phenology was related to the location of the wintering areas in our study. The most southerly wintering study species were the earliest to arrive in autumn, which highlights the role of the distance to the wintering grounds. The longest distances to their wintering grounds are covered by Arctic Warblers and Two-barred Warblers,

which might be the cause for the early autumn migration at the study site. Pallas's Leaf Warblers have a rather short distance to cover between the breeding and wintering areas, which may explain its late migration in autumn (del Hoyo et al. 2006). Consequently, the opposite pattern was found in spring, with species migrating shorter distances arriving earlier than those species with wintering grounds further south. Similar patterns are known from songbirds in other flyway systems (Alerstam 1993). Even within species, northern populations are known to migrate longer distances and to occur later on stop-over sites, e.g., in Eurasian Blackcap *Sylvia atricapilla* (e.g., Lövei et al. 1985), Garden Warbler *Sylvia borin* (Berthold 1988), Common Chiffchaff *P. collybita* (Gaston 1974; Tiainen and Hanski 1985) and Willow Warbler *P. trochilus* (Hedenström and Pettersson 1987).

Despite the fact that departure in autumn depends on the length of the breeding season (Ellegren 1990; Fransson 1995), we found no effect of the end of the breeding period on the timing of migration in our study. This may be due to the fact that the studied species typically have only one brood annually due to the short time available for hatching (del Hoyo et al. 2006), so there might be no significant variation among the species.

Furthermore, we found that migration periods are longer in autumn than in spring for all of our study species. This is most likely caused by the fact, that competition is high to arrive early at the breeding grounds in spring and, therefore, the migration is faster in spring than in autumn (Karlsson et al. 2012; Nilsson et al. 2013). We found the smallest species (Pallas's Leaf Warbler and Yellow-browed Warbler) to arrive earliest in spring. Gaston (1974) hypothesized that small *Phylloscopus* species breed earlier than larger species, and by wintering farther north they can rapidly return to the breeding grounds. This might be true for the species

in our study as well, although no obvious differences in the start of breeding are evident (Table 1). Some early breeding, small species make very long migratory journeys (to Northern Siberia from Southeast Asia) (Gaston 1974), suggesting that wintering far away does not necessarily prevent an early return to breeding grounds (Katti and Price 2003).

## Conclusion

We identified moult strategy and the preferred prey size as the most important factors shaping spring phenology, while the position of the wintering areas was related to autumn migration phenology in Siberian leaf warblers. The migration periods of our study species were significantly shorter in spring than in autumn. These results are in line with findings from other flyway systems. Our work contributes to a better understanding of the causes and consequences of the migration of little-known East Asian songbird species.

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**Author contributions** LB and WH designed the project. LB and WH conducted field work and data collection. WH and LB analysed the data and wrote the manuscript. LB, WH and TCS interpreted the results. LB, WH and TCS edited the manuscript. All authors read and approved the last version of the manuscript.

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**Code availability** Not applicable.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Availability of data and material** The datasets analysed during the current study are available from the corresponding author on reasonable request.

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