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Weather conditions affect spring and autumn migration of Siberian leaf warblers

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Abstract

Background: Weather effects on bird migration are well-studied among Passerines moving from Europe to Africa or within the American flyway systems. However, little is known about the weather impact on songbirds migrating along the East Asian flyway. Our study aims to describe the effects of various weather elements on the migration of four species of leaf warblers by using bird ringing data from a stopover site in Far East Russia.

Methods: We determined the migration periods for each species and included maximum temperature, precipitation, air pressure, wind speed and wind direction in general linearized mixed models to predict the number of migrating birds.

Results: We found strong impacts of weather variables on the number of trapped warblers during spring and autumn migration. Preferred or avoided weather conditions were similar among the studied species. All species seem to migrate preferably during warm, calm days without precipitation. A positive effect of tail winds was only confirmed in autumn, but in spring, most birds were trapped during crosswinds (eastern or western winds).

Conclusion: The studied species might exhibit a loop migration, leading to a more longitudinal (from east to west) migration pattern in our study area during spring. Relationships between weather variables and the number of migrating individuals were much stronger during autumn. We argue that birds during spring migration would continue migration under sub-optimal conditions, as a result of strong competition to arrive earliest on their breeding grounds.

Keywords: *Phylloscopus*, Bird migration, Weather, East Asian flyway

Background

During migration birds face many challenges, including unfamiliar foraging and refuge habitats, resulting in a much higher rate of mortality during migration than during other seasons of the year. Weather may significantly affect a bird's decision to initiate migration, the course and pace of migration, and its survival during migration (Miller et al. 2016). Favourable weather conditions for migration enhance the orientation of birds, reduce the use of energy for flying and increase the speed of migration (Emlen 1975; Bloch and Bruderer 1982; Gauthreaux 1982; Akesson 1993; Liechti 2006; Shamoun-Baranes et al. 2017). According to the majority of the studies,

most migrations take place in windless, clear, anticyclonic weather conditions without precipitation, or with support of tail winds (Alerstam 1990; Gyurácz et al. 1997, 2003; Bruderer and Boldt 2001; Erni et al. 2002). Favourable conditions can occur in different macrosynoptic weather situations (Kerlinger et al. 1989). Atmospheric conditions are the primary extrinsic factors influencing decisions regarding migratory flights, particularly over water bodies with limited opportunities to land (Richardson 1990). Wind plays a critical role, affecting departure date and migratory directions, routes, speeds, flight durations, energy consumption and the crossing of ecological barriers (Cochran and Kjos 1985; Weber and Hedenström 2000; Pennycuick and Battley 2003; Cochran and Wikeski 2005; Bowlin and Wikelski 2008; Shamoun-Baranes and van Gasteren 2011; Bulte et al. 2014; Gill et al. 2014). Decisions to depart stopover sites and initiate

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flight over large water bodies are also influenced by barometric pressure, temperature, relative humidity, and short-term trends in these variables, which are indicative of synoptic weather patterns and may provide information about future weather conditions (Able 1972; Newton 2008). In case of tail winds, birds are capable of flying longer distances while exerting less energy (Emlen 1975; Bloch and Bruderer 1982; Gauthreaux 1982, 1991; Alerstam 1990; Richardson 1990; Bruderer and Boldt 2001). Weather conditions that delay migration include cloudy skies, poor visibility, strong winds (head winds and cross winds), and warm or occluded fronts (Akesson 1993; Pyle et al. 1993).

The relationship between the migration of birds and various weather elements or atmospheric conditions was studied mostly in Europe (Alerstam 1978, 1990; Akesson 1993; Erni et al. 2002; Schaub et al. 2004; Van Belle et al. 2007; Arizaga et al. 2011) and North America (Able 1973; Emlen 1975; Kerlinger et al. 1989; Deppe et al. 2015; Woodworth et al. 2015). However, few studies are available for the migration of Siberian species, providing only limited information on autumn and spring migration phenology of some species (Williams 2000; Bozó and Heim 2015, 2016; Bozó et al. 2016, 2017; Sander et al. 2017), or focussing on their (irregular) occurrences in Europe (Rabøl 1969; Baker 1977; Folvik 1992; Berthold 1996; Thorup 1998, 2004; Phillips 2000; Gilroy and Lees 2003; Krüger and Dierschke 2004; Harrop 2007; De Juana 2008; Jiguet and Barbet-Massin 2013). However, to understand the causes of the European vagrancies, information on migration phenology of this species related to local weather is necessary. Expanding this knowledge is not only important in understanding the causes of their vagrancy, but also for perspective conservation measures. Some of the East Asian migrants have declined dramatically (Kamp et al. 2015), and local declines are noted even in common species, e.g. in wintering Yellow-browed Warblers (*Phylloscopus inornatus*) on Hainan Island (Xu et al. 2017).

This study aims to describe the effects of various weather elements on the numbers of migrating Siberian breeding *Phylloscopus* warbler species at a stopover site in Far East Russia.

Methods

The study was carried out within the Amur Bird Project during spring (2013, 2015, 2016, 2017) and autumn (2011–2014) migration at Muraviovka Park along the middle stream of the Amur River in the Russian Far East (Heim et al. 2012). The study site is located 60 km southeast of the city of Blagoveshchensk (49°55′08.27″N, 127°40′19.93″E).

The study periods were the following: in 2011, from 7 September to 15 October; in 2012, from 29 August to 15 October; in 2013, from 25 April to 08 June and from 27 July to 17 October; in 2014, from 25 July to 15 October; in 2015, from 25 April to 10 June; in 2016, from 25 April to 07 June, while in 2017, from 28 April to 08 June. During this period, in total 52 mist-nets were used for the work. Netting sites were not changed within season, however, the sampling effort varied among years (Table 1). The nets were set up in a variety of habitats: homogeneous reed-beds, sedges and grassy swamps interspersed with willows and raspberries, rich shrub-layered mixed forest, very dense scrub and stubble. The work was carried out daily from sunrise to sunset and the nets were checked every hour. In case of storm, heavy wind and rain, nets were closed.

Data analysis was carried out based on 6191 individuals of four species: Yellow-browed Warbler (*Phylloscopus inornatus*), Dusky Warbler (*P. fuscatus*), Radde's Warbler (*P. schwarzi*) and Pallas's Leaf Warbler (*P. proregulus*) (Table 2). All birds were marked with rings of the Moscow Ringing Centre. Species identifications were based on Svensson (1992) and Brazil (2009). We only included data of first captures and excluded all recaptures.

To analyse the effects of weather for bird migration, we collected the following weather data for every day: minimum and maximum temperature (°C), precipitation (mm), average air pressure (mb), average wind speed (Beaufort scale 0–12), average wind direction (cross winds: E and W winds in spring and autumn; tail winds: N, NE and NW in autumn and S, SE and SW in spring; head winds: N, NE and NW in spring and S, SE and SW in autumn). Air pressure and precipitation data were gathered from the webpage of World Weather Online (World Weather Online 2017) for the area of Blagoveshchensk, while the remaining data were collected by the ringing teams at Muraviovka Park.

Table 1 Sampling effort between 2011–2017 at the study site (total number of nets × daily mist-netting hours)

Year	Season	
	Spring	Autumn
2011	–	6161
2012	–	14,253
2013	9352	16,654
2014	–	31,235
2015	8204	–
2016	6710	–
2017	7729	–

Table 2 Number of ringed birds for all study species and their migration periods at Muraviovka Park

Species	Number of birds		Migration period	
	Spring	Autumn	Spring	Autumn
Yellow-browed Warbler	2275	1584	26 April–6 June	26 July–13 October
Dusky Warbler	497	1089	29 April–9 June	26 July–9 October
Pallas’s Leaf Warbler	79	369	29 April–5 June	6 September–17 October
Radde’s Warbler	81	217	9 May–8 June	5 August–26 September

The migration periods are species-specific, therefore it was necessary to determine migration periods for each species. On the basis of the daily numbers caught, migration periods were determined for all studied species (Fig. 1). Only days within the migration period were considered in the following models.

General Linear Mixed Models (GLMM) were used to evaluate the weather impact on the number of trapped birds per day. Models were built for each species for both spring and autumn season. Year and Julian day were included as random factors. Minimum temperature was excluded from the models, as it was highly correlated with maximum temperature ($R=0.77$, $t=30.2$, $df=722$, $p<0.001$). The full models were of the following structure:

$$\begin{aligned} &\text{the number of birds trapped per day} \\ &\sim \text{temperature} + \text{precipitation} + \text{air pressure} \\ &+ \text{wind speed} + \text{wind direction} + 1 | \text{year} + 1 | \text{day}. \end{aligned}$$

Furthermore, we built a model for all four species together, and included species as additional random factor as well. We checked for overdispersion using the dispersion-glmmer function of the R package blmeo. For

analysis, R version 3.4.2 (R Core Team 2017) and packages lme4 (Bates et al. 2014) and piecewiseSEM (Lefcheck 2016) were used.

Results

The migration periods of the four study species are shown in Table 2.

The GLMM for single species explained only a small part of the variability, with higher values during autumn migration (R^2_{marg} : 0.07–0.18) compared to spring migration (R^2_{marg} : 0.03–0.10). This was also true for the overall model, including all four species—see Table 3. Much more of the variance was explained by the random factors (R^2_{cond}) (Table 3).

During spring, the most important factor for all species is temperature, with significantly more birds trapped during warmer days. Furthermore, wind direction is a significant predictor in the overall model and in two out of four species models, with the highest number of birds trapped during cross winds.

In autumn, the number of trapped warblers is negatively affected by precipitation and wind speed, while maximum temperature is positively related with the number of trapped individuals in the overall model and

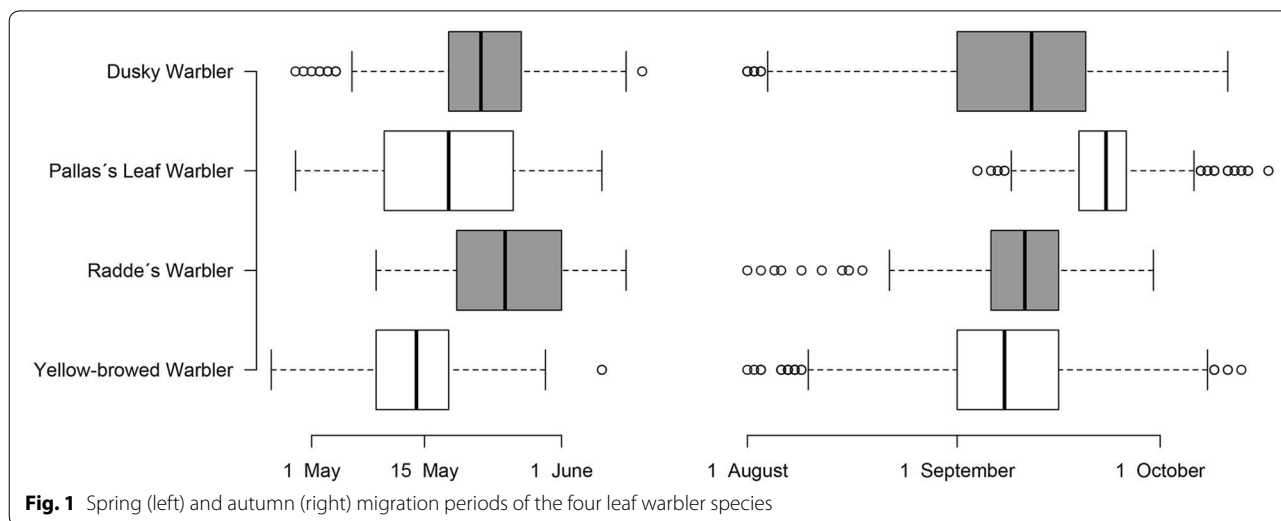


Fig. 1 Spring (left) and autumn (right) migration periods of the four leaf warbler species

Table 3 Outputs of general linear mixed models

Species		Spring migration			Autumn migration			
		Estimate	χ^2	<i>p</i>	Estimate	χ^2	<i>p</i>	
ALL	Temperature	0.42	133.3	***	Temperature	0.22	18.4	***
	Precipitation	0.09	8.7	0.003	Precipitation	−0.53	121.4	***
	Air pressure	−0.10	9.4	0.002	Air pressure	−0.25	39.3	***
	Wind speed	0.09	9.3	0.002	Wind speed	−0.29	65.6	***
	Wind direction		65.8	***	Wind direction		54.6	***
	<i>Headwind</i>	−0.30			<i>Headwind</i>	−0.39		
	<i>Crosswind</i>	−0.05			<i>Crosswind</i>	−0.17		
	<i>Tailwind</i>	−0.72			<i>Tailwind</i>	0.08		
	<i>R</i> ² _{marg}	0.03			<i>R</i> ² _{marg}	0.12		
	<i>R</i> ² _{cond}	0.82			<i>R</i> ² _{cond}	0.84		
Dusky Warbler	Temperature	0.41	17.0	***	Temperature	0.35	16.9	***
	Precipitation	0.09	1.0	0.321	Precipitation	−0.50	37.7	***
	Air pressure	−0.01	0.0	0.861	Air pressure	−0.13	4.3	0.039
	Wind speed	0.08	1.0	0.310	Wind speed	−0.09	2.4	0.121
	Wind direction		17.0	***	Wind direction		18.8	***
	<i>Headwind</i>	0.42			<i>Headwind</i>	0.29		
	<i>Crosswind</i>	1.12			<i>Crosswind</i>	0.53		
	<i>Tailwind</i>	0.08			<i>Tailwind</i>	0.76		
	<i>R</i> ² _{marg}	0.09			<i>R</i> ² _{marg}	0.18		
	<i>R</i> ² _{cond}	0.75			<i>R</i> ² _{cond}	0.84		
Pallas's Leaf Warbler	Temperature	0.40	5.2	0.022	Temperature	−0.27	2.3	0.126
	Precipitation	0.01	0.0	0.946	Precipitation	−0.24	2.2	0.137
	Air pressure	−0.03	0.0	0.870	Air pressure	0.10	0.7	0.417
	Wind speed	0.02	0.0	0.900	Wind speed	−0.43	13.1	***
	Wind direction		4.7	0.096	Wind direction		6.3	0.043
	<i>Headwind</i>	−1.11			<i>Headwind</i>	−2.05		
	<i>Crosswind</i>	−0.34			<i>Crosswind</i>	−1.74		
	<i>Tailwind</i>	−1.35			<i>Tailwind</i>	−1.51		
	<i>R</i> ² _{marg}	0.09			<i>R</i> ² _{marg}	0.07		
	<i>R</i> ² _{cond}	0.34			<i>R</i> ² _{cond}	0.71		
Radde's Warbler	Temperature	0.56	8.9	0.003	Temperature	0.38	5.9	0.016
	Precipitation	0.00	0.0	0.993	Precipitation	−0.45	8.5	0.004
	Air pressure	0.01	0.0	0.932	Air pressure	−0.54	16.2	***
	Wind speed	0.13	0.7	0.399	Wind speed	−0.27	16.2	0.022
	Wind direction		2.5	0.292	Wind direction		6.3	0.043
	<i>Headwind</i>	−1.12			<i>Headwind</i>	−2.07		
	<i>Crosswind</i>	−1.17			<i>Crosswind</i>	−1.41		
	<i>Tailwind</i>	−1.67			<i>Tailwind</i>	−1.77		
	<i>R</i> ² _{marg}	0.10			<i>R</i> ² _{marg}	0.13		
	<i>R</i> ² _{cond}	0.44			<i>R</i> ² _{cond}	0.70		
Yellow-browed Warbler	Temperature	0.44	118.6	***	Temperature	0.21	7.5	0.006
	Precipitation	0.09	7.1	0.008	Precipitation	−0.57	68.7	***
	Air pressure	−0.14	16.4	***	Air pressure	−0.32	24.6	***
	Wind speed	0.08	6.6	0.010	Wind speed	−0.45	71.3	***
	Wind direction		46.1	***	Wind direction		27.6	***
	<i>Headwind</i>	0.98			<i>Headwind</i>	0.39		
	<i>Crosswind</i>	1.12			<i>Crosswind</i>	0.59		
	<i>Tailwind</i>	0.57			<i>Tailwind</i>	0.89		
	<i>R</i> ² _{marg}	0.03			<i>R</i> ² _{marg}	0.18		
	<i>R</i> ² _{cond}	0.94			<i>R</i> ² _{cond}	0.92		

Table 3 (continued)

Estimates refer to the slope related to the variables, but represent the mean for categorical variables (wind direction, in italics). Shown are test statistics, R_{marg}^2 (fixed factors alone) and R_{cond}^2 (fixed + random factor). p values below 0.001 are marked as ***

in three out of four species. Wind direction is an important factor in all models, with most birds trapped during tail wind, and least birds during head winds. Air pressure was found to have minor impact on the numbers, but a negative relation was found in three out of four species.

Discussion

During our work, the effects of air pressure, rainfall, temperature, wind strength and wind direction were investigated for four species. We found strong impacts of weather variables on the number of trapped warblers during spring and autumn migration. Overall, preferred or avoided weather conditions were similar among the studied species, but some slight differences were found.

All species seem to migrate preferably during warm, calm days without precipitation in spring and autumn too. It is important to note that in case of intense rainy weather, mist-nets were closed for the safety of the birds, but there would certainly not have been a significant amount of bird in these days. The fact, that the maximum temperature is positively related with the number of trapped individuals in the overall model and in three out of four species is certainly associated with the timing of migration.

Previous studies have shown that the migration peak of most species coincides with days of high air pressure (Alerstam 1990; Gyurácz et al. 1997). On such days, there is constant sunshine and low temperatures. In Siberia, a high anti-cyclone reigns from September to April, with its centre near Lake Baikal. This Siberian cycle is often characterized by high air pressures above 1040 mb and extremely low temperatures (Oliver 2005). In spring, however, the effects of cyclones are characterized by high precipitation and high temperature values. In contrast, air pressure was found to have minor impact on the numbers of trapped warblers both during spring and autumn migration, but a slight negative relation was found in three out of four species in autumn. This suggests that the studied species seem to migrate independently from the air pressure.

Both the strength and the direction of the wind can be decisive in the timing of migration (Elkins 1988). In stormy winds, mist-netting is not possible, but as during heavy rains, few birds are expected to fly during such conditions. Accordingly, the number of birds of all species and the strength of wind were negatively correlated in spring and autumn migration.

In autumn, in cases of a northerly wind (tail wind), birds are known to fly longer distances while exerting

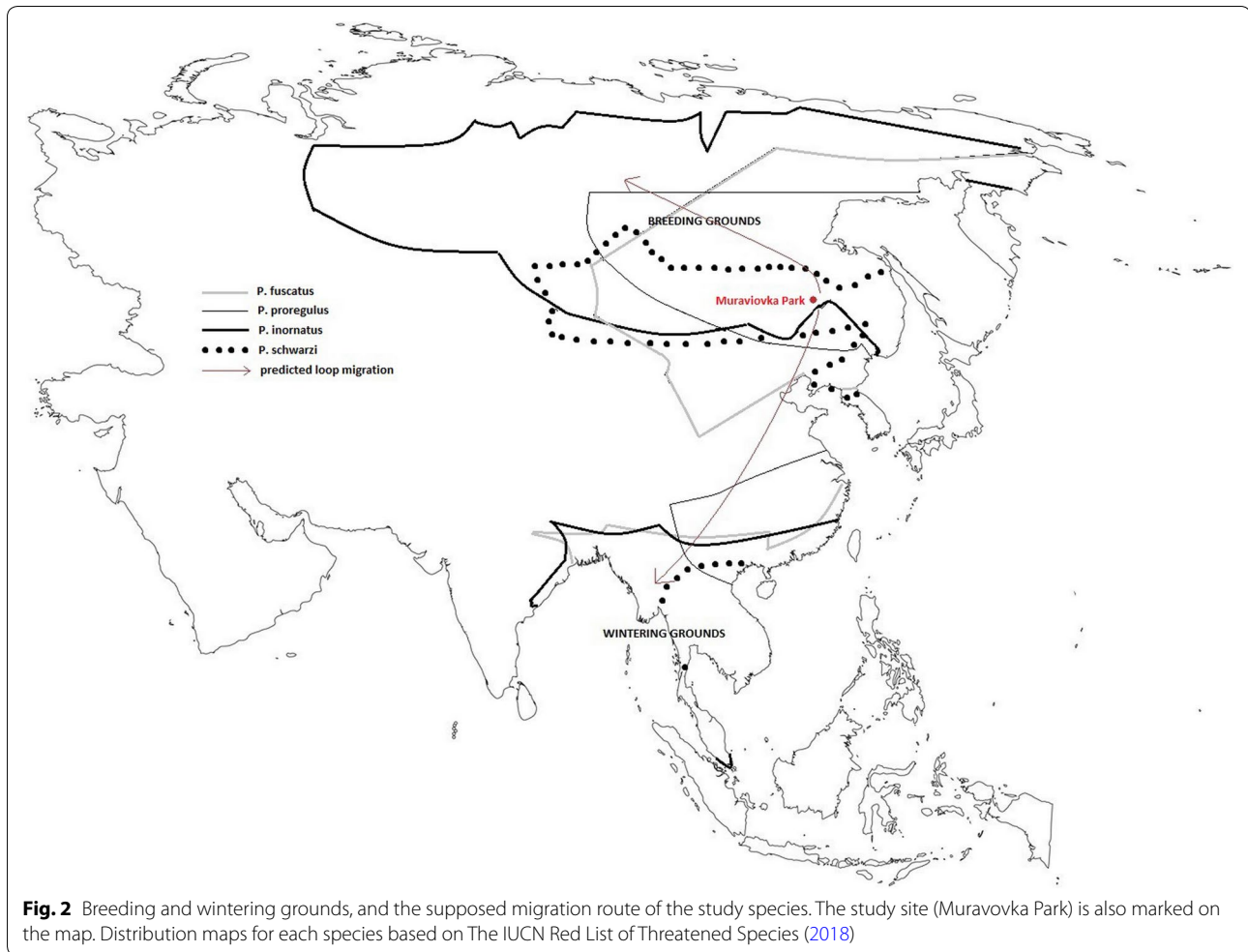
less energy (Emlen 1975; Bloch and Bruderer 1982; Gauthreaux 1982, 1991; Alerstam 1990; Richardson 1990). Accordingly, we would expect the highest numbers of migrating birds in autumn during northern tail winds and in spring during southern tail winds. However, a positive effect of tail winds was only confirmed in autumn. Tail winds were a good predictor in case of Dusky and Yellow-browed Warblers in autumn, which may support the weather hypothesis, according to which some authors explain the westward vagrancy of Siberian leaf warblers species by the effect of the weather (Baker 1977; Howey and Bell 1985; Baker and Catley 1987). It is interesting to note that in spring, most birds were trapped during cross winds (eastern or western winds). It seems likely, that the studied warbler species exhibit a loop migration, with their spring migration routes closer to the East Asian coasts, leading to a more longitudinal migration pattern (from east to west) in our study area during spring (Fig. 2). The Wood Warbler (*Phylloscopus sibilatrix*) and Willow Warbler (*Ph. trochilus*), well-studied European breeding species, show also loop migration (Gyurácz and Csörgő 2009; Jónás et al. in press), and a similar pattern was found for geolocator-tracked Siberian Rubythroats (*Calliope calliope*) along the East Asian flyway (Heim et al. 2018a).

Despite the significant impacts of the weather variables, most of the variation was explained by interannual differences and preferred migration timing. The studied species are likely mainly following their innate migration schedule. Consistent migration timing between years was also found for *Emberiza* buntings at our study site (Heim et al. 2018b). This might especially be true for spring migration, when competition is high to arrive early at the breeding grounds (Nilsson et al. 2013), which could force individuals to continue migration under sub-optimal weather conditions.

Global change is expected to significantly alter weather conditions in Far East Russia (Mokhov and Semenov 2016) and a better understanding of how these factors could influence migratory birds is urgently required.

Conclusion

During our work we found strong impacts of weather variables (air pressure, rainfall, temperature, wind strength and wind direction) on the number of trapped warblers during spring and autumn migration. Birds seem to migrate preferably during warm, calm days without precipitation, however, relationships between weather variables and the number of migrating individuals were much



stronger during autumn. Air pressure was found to have minor impact on the numbers of trapped warblers, while the strength and the direction of wind were important variables. Tail winds play an important role in autumn, but in spring migration was determined by cross winds, which indicates that the studied species might exhibit a loop migration.

Authors' contributions

LB and WH collected field data. TCS provided new ideas for this manuscript. LB and WH performed data analyses. LB collected the weather data from the online dataset. LB wrote an early version of the manuscript. WH and TCS revised and improved the manuscript. All authors read and approved the final manuscript.

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Acknowledgements

The authors want to thank Sergei M. Smirenski and the staff of Muraviovka Park as well as the Amur Bird Project field teams for enabling these studies in Far East Russia. We kindly acknowledge the provision of rings by the Moscow Bird Ringing Centre, and thank Ramona J. Heim and Johannes Kamp for helpful comments on the statistical analysis.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

The authors confirm that all experiments were carried out under the current law for scientific bird ringing in Russia, and all necessary permissions were obtained.

Funding

The bird ringing program was supported by the German Ornithologists' Society, the Förderkreis Allgemeine Naturkunde (Biologie) e.V. and the NABU RVE e.V. LB's work was supported by the Campus Hungary Studentship and the Hungarian National Young Talent Studentship.

Received: 8 April 2018 Accepted: 11 October 2018
Published online: 17 October 2018

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