

Article

Migration phenology determines niche use of East Asian buntings (Emberizidae) during stopover

Wieland HEIM^{a,*}, Jana A. ECCARD^b, and Franz BAIRLEIN^c

^aInstitute of Landscape Ecology, Münster University, Heisenbergstraße 2, Münster, 48149, Germany, ^bAnimal Ecology, Institute of Biology and Biochemistry, Universität Potsdam, Maulbeerallee 1, Potsdam, 14469, Germany,

^cInstitute of Avian Research “Vogelwarte Helgoland”, An der Vogelwarte 21, Wilhelmshaven, 26386, Germany

*Address correspondence to Wieland Heim. E-mail: wieland.heim@uni-muenster.de.

Received on 26 September 2017; accepted on 25 January 2018

Abstract

Stopover niche utilization of birds during migration has not gained much attention so far, since the majority of the studies focuses on breeding or wintering areas. However, stopover sites are crucial for migratory birds. They are often used by a multitude of species, which could lead to increased competition. In this work, we investigated niche use of 8 migratory and closely related *Emberiza* bunting species at a stopover site in Far East Russia, situated on the poorly studied East Asian flyway. We used bird ringing data to evaluate morphological similarity as well as niche overlap on the trophic, spatial, and temporal dimension. Bill morphology was used as a proxy for their trophic niche. We were able to prove that a majority of the species occupies well-defined stopover niches on at least one of the dimensions. Niche breadth and niche overlap differ between spring and autumn season with higher overlap found during spring. Morphological differences are mostly related to overall size and wing pointedness. The temporal dimension is most important for segregation among the studied species. Furthermore, all species seem to exhibit a rather strict and consistent phenological pattern. Their occurrence at the study site is highly correlated with their geographic origin and the length of their migration route. We assume that buntings are able to use available resources opportunistically during stopover, while trying to follow a precise schedule in order to avoid competition and to ensure individual fitness.

Key words: bird migration, *Emberiza*, habitat use, non-breeding, phenology, stopover.

Introduction

Migratory flights are energetically costly (Wikelski et al. 2003). Consequently, many migratory birds do need to replenish energy stores during migration at intermittent stopover sites (Klaassen 1996). At such stopover sites, migrants often share space with other con- and heterospecific birds. How different species of stopover migrants share space has rarely been studied in detail (Kober and Bairlein 2009) which is in particular so for Asian migrants. Ecological niche segregation is a way different species may share a stopover site.

In general, an ecological niche is usually defined as the range in which a species can have positive population growth (Chase 2011).

Those niches are shaped by competition with other species, resulting in segregation or resource partitioning (Pianka 1981). The niche concept itself dates back to Grinnel (1917) and is now widely applied in bioecology and sociology (Popielarz and Neal 2007). Segregation can be found on different dimensions (Pianka 1981): there can be temporal niches (for example, Carothers and Jaksic 1984; Kronfeld-Schor and Dayan 2003; Castro-Arellano and Lacher 2009; Hayward and Slotow 2009), spatial niches (Hagen et al. 2007), trophic niches (Dammhahn et al. 2015), acoustic niches (Henry and Wells 2010), or niches defined by light intensity (Gerrish et al. 2009). In many cases, a combination of different dimensions was found to be relevant (Pianka

1973; Piet et al. 1999; Albrecht and Gotelli 2001; Gilbert et al. 2008; Dennis and Hellberg 2010). The more species are included, the more dimensions have to be considered, on which species might segregate: if species are similar on 1 dimension, dissimilarity on another dimension should be implied (Schoener 1974). However, even species inhabiting an identical niche can coexist in highly structured food webs (Leibold and McPeck 2006). This can be explained by stochastic effects and might be driven by dispersal instead of competition—the basic assumption of the “neutral theory” (Leibold 2008). The debate remains open whether niche partitioning, neutrality, or a synthesis of both is the key for species diversity (Moullot 2007; Leibold 2008; Vergnon et al. 2009). In recent studies, both theories were included in models explaining species diversity (Haegeman and Loreau 2011; Ai et al. 2013; Munoz et al. 2014).

Niches are highly dynamic on temporal and spatial scales, and can change between seasons—which might be especially true for most migratory birds, covering thousands of kilometres between breeding grounds, stopover sites, and wintering areas twice a year (Bairlein et al. 2012). Niche utilization and segregation during breeding season is well described for many species of birds (e.g. Kosiński and Winięcki 2004; Kaboli et al. 2007; Laughlin et al. 2013). However, information is scarce for stopover sites used during the long period of migration. Explanations for the coexistence of migrants and residents in those areas are largely lacking (Salewski and Jones 2006), but see Bensusan et al. (2011). It has been shown that many migrants “track” their niche, instead of switching it during the non-breeding season (Joseph and Stockwell 2000; Nakazawa et al. 2004; Papes et al. 2012). On the other hand, changes in niche utilization between seasons have been shown for migratory *Sylvia* warblers (Laube et al. 2015). Overlapping niches have been found during times of low food supply (Jędrzejewski et al. 1989; Hasui et al. 2009) or superabundance of high quality food (Choi et al. 2017). Niche segregation at stopover sites can also be hampered under poor food conditions, when individuals have to utilize a broader range of available niches (Kober and Bairlein 2009). In *Uria* murrelets, it was also found that sympatric species “widened” their niches during non-breeding season to avoid competition (McFarlane Tranquilla et al. 2015).

Moreover, niche segregation may vary with season. Spring migration of many bird species often differs from their autumn journeys and shows higher migration speed and a lower number of stopovers (Schmaljohann et al. 2012; Nilsson et al. 2013). Also the time window, in which nocturnal migrants initiate their flights, is smaller during spring migration (Bolshakov et al. 2007; Schmaljohann et al. 2011). These restrictions might also cause differences in niche use and niche overlap between seasons.

Past studies on niche use outside breeding season focused on waders (Davis and Smith 2001; Burger et al. 2007; Jing et al. 2007; Kober and Bairlein 2009; Bocher et al. 2014) as well as penguins (Wilson 2010; Hinke et al. 2015) and seabirds (Young et al. 2010; Quillfeldt et al. 2013; McFarlane Tranquilla et al. 2015; Orben et al. 2015; Quillfeldt et al. 2015), whereas studies on songbirds are scarce (Bairlein 1983, 1992; Martinez-Meyer et al. 2004; Laube et al. 2015) and are virtually absent for the East Asian flyway (Yong et al. 2015). This flyway, however, holds the highest diversity of migratory birds, including numerous threatened species (Yong et al. 2015). The group of buntings (Emberizidae) has currently gained global conservation interest caused by catastrophic declines of several species of the genus *Emberiza* in Europe and Asia (Menz and Arlettaz 2012; Kamp et al. 2015; Edenius et al. 2017). Far East Russia is the diversity hotspot of this threatened genus (Päckert et al. 2015). Knowledge of their specific needs and niches throughout the

Table 1. Study species and number of trapped birds (including retraps), 2011–2016 ($n = 7642$)

English name	Scientific name	Number of trapped birds		
		Spring	Autumn	Other
Yellow-breasted Bunting	<i>Emberiza aureola</i>	1	19	50
Yellow-browed Bunting	<i>E. chrysophris</i>	63	145	187
Meadow Bunting	<i>E. cioides</i>	2	0	0
Yellow-throated Bunting	<i>E. elegans</i>	174	73	101
Chestnut-eared Bunting	<i>E. fucata</i>	0	0	32
Pine Bunting	<i>E. leucocephalos</i>	1	19	24
Pallas's Reed Bunting	<i>E. pallasi</i>	53	181	647
Little Bunting	<i>E. pusilla</i>	96	288	753
Rustic Bunting	<i>E. rustica</i>	103	210	543
Chestnut Bunting	<i>E. rutila</i>	6	63	67
Common Reed Bunting	<i>E. schoeniclus</i>	1	5	21
Black-faced Bunting	<i>E. spodocephala</i>	578	959	1985
Tristram's Bunting	<i>E. tristrami</i>	9	3	15
Ochre-rumped Bunting	<i>E. yessoensis</i>	4	51	108
Lapland Bunting	<i>Calcarius lapponicus</i>	0	0	1
Snow Bunting	<i>Plectrophenax nivalis</i>	0	0	1

Individuals trapped using standard nets during spring (April–June 2013, 2015, 2016) and autumn (August–October 2013–2015) migration as well as birds trapped during breeding season or with non-standard nets (“Other”) are shown separately.

annual cycle will be crucial for their conservation (Newton 2004; Bairlein 2016). In this study, we analyze niche use and niche segregation during stopover among a group of closely related bunting species. In doing so, we want to prove the hypotheses listed below:

1. There are well-defined stopover niches—all species differ on at least 1 niche dimension.
2. Niche utilization and overlap differs between spring and autumn migration.
3. The temporal dimension is the most important, since trophic and spatial niches can be widened during stopover.
4. The occurrence of a species at the stopover site is linked to its geographic origin (latitude).

Materials and Methods

Data were collected within the Amur Bird Project, a standardized bird-ringing scheme at Muraviovka Park (49°55'08", 27°N, 127°40'19", 93°E) in Far East Russia (Heim et al. 2012; Heim and Smirenski 2013). Such ringing data were proven to be suitable for characterization of migration phenology (Knudsen et al. 2007). Birds were trapped during spring (April–June) and autumn (August–October) migration 2011–2016. Additional individuals were ringed during breeding season 2013–2016. A total of 7,642 trapped individuals of 16 species were available for analysis (Table 1). All statistical analysis were carried out using the program R version 3.2.4 (R Core Team 2016).

Morphology

East Asian buntings show sexual size dimorphism, with males being bigger, longer winged and longer tailed (Nam et al. 2011). Therefore, 15 males and 15 females each were randomly selected for each study species. To avoid ringer-specific differences, only individuals which have been measured by the first author were considered,

with few exceptions for single Chestnut Buntings *Emberiza rutila*, Ochre-rumped Buntings *E. yessoensis*, and Little Buntings *E. pusilla*. All measurements were taken as proposed by Eck et al. (2011): Wing length (Wmax), Wing pointedness (Kipp-Index), Tail length, Bill length (Bsk), Bill width (Bwp), and Bill depth (Bp). Birds were weighed with a precision to 0.1 g using an electronic weight (Ecotone Pesola PPS200). As age determination was not always possible, both adults and first-year birds were included in this study. A principal component analysis (PCA) was used to investigate which morphological features contribute most to the interspecific variability. All data were standardized using a log transformation, to minimize the effects of different units (Shao et al. 2016). In our first PCA, data were not size corrected to preserve the valuable information of body size, which could act as an important factor for species segregation (Alatalo et al. 1986; Shao et al. 2016). In our second PCA, data were size corrected by dividing all measures of length by the cube root of lean body mass to analyze differences in shape (Winkler and Leisler 1992). Bill morphology was used as a proxy for the size of the feeding structure—which is usually correlated to food characteristics (Schoener 1965, 1974). Similarity among species was described based on difference in wing, tail, and tarsus length as well as bill morphology applying the method of Ricklefs and Cox (1977). We computed an index of overall similarity as well as an index of bill similarity accordingly.

Habitat and phenology

There are known differences in migratory behavior among sexes—especially during spring migration, when males often migrate ahead of the females (Schmaljohann et al. 2016). The occurrence of the so-called protandrous migration in East Asian buntings was shown by Nam et al. (2011) at a stopover site on the Korean Peninsula, and was also found in Ortolan Bunting *E. hortulana* along the west end of the Asian continent (Yosef and Tryjanowski 2002). To allow for inner-specific variation, we included all species where we had a sufficient sample size for both females and males in our study. We included all species in the analysis with a sample size of $n > 30$ per season. For the analysis of habitat use and phenology we included those periods, during which all nets were opened at exactly the same locations for the same time span. This was true for the spring seasons in 2013, 2015, and 2016 from April to June and for the autumn season during the years 2013–2015, when trapping was conducted from the beginning of August until the end of October. A total of 17 nets with lengths of either 6 ($n = 4$) or 12 m ($n = 13$) was used. Each net was assigned to 1 of 6 different types of habitats, which form a gradient from the low wetlands to the forests on the river terrace. Habitat type A (reed) consists of reed stands with *Phragmites australis* and *Carex spec.* Habitat type B (willow1) is characterized by low willow thickets (for example, *Salix miyabeana*) and wet meadows. Habitat type C (willow2) is situated on the edge of the river terrace and includes larger willow bushes and trees (e.g. *S. pierotii*). Habitat type D (deciduous) is situated on the terrace, with poplar *Populus tremula* and bird cherry *Prunus padus* trees and raspberry *Rubus idaeus* in the understorey. Large Mongolian oak *Quercus mongolica* trees are characteristic for Habitat type E (oak), as well as a dense understorey with *Artemisia spec.* and *Lespedeza bicolor*. A pine plantation with *Pinus sylvestris* forms Habitat type F (pine). Habitats A–C are situated in the lowlands, and Habitats D–F on the terrace. The nets were not equally distributed among the habitat types, for details see Supplementary Material 1. χ^2 -tests were used to evaluate whether the trapped buntings are randomly distributed among the habitat types and whether there are differences between

seasons in the relative abundance of the species and the habitats used. Null hypothesis (random distribution) was rejected if $P < 0.05$. Habitat use was compared between species with a cluster analysis (Ward method based on Euclidean distances).

In 2013, an extreme flood event occurred, covering the floodplain completely with water for the first time since 30 years (Sokolova 2015). Therefore, the conditions at the nets in the wetlands changed drastically, and mist-net sites in Habitat type B were completely drowned. Habitat use (abundance of trapped birds per habitat type) differed significantly between the flood year and the years without flood ($\chi^2 = 159.89$, $df = 5$, $P < 0.001$). Therefore, we excluded the year 2013 for the analysis of habitat use.

We adopted the approach Bairlein (1981) used to compute niche breadth, since we intend to describe the species-specific relative utilization of the resources at the study site. For the analysis of niche overlap, we used the R package spaa (Zhang 2016) with the widely used niche overlap measure based on Pianka (1973). Niche overlap in phenology was computed based on the proportion of birds trapped per calendar week during spring and autumn migration. We used a Pearson's product moment correlation to investigate the relationship between mean migration days during spring and autumn. Differences in phenology between years were tested with simple linear models (Day~Year). Linear mixed-effects models (LMEs) were used to analyze the impact of different variables on migration timing. This analysis was carried out with R package nlme (Pinheiro et al. 2016). The following variables were used to explain the dependent variable *median migration day* for spring and autumn each: *breeding latitude* (*southernmost*, *northernmost*), *wintering latitude* (*southernmost*, *northernmost*) and *migration distance* (length of migration route calculated as difference between mean breeding and wintering latitude). Information about distribution of bunting species was gathered from the BirdLife range maps (BirdLife International 2017), see Supplementary Material 2. The application of LMEs allowed us to include *year* and *species* as random factors. Significant variables were selected with help of “backward stepwise model selection” (Crawley 2013) using the Likelihood-ratio test ($P < 0.05$) and the Akaike information criterion (AIC)-values. Normal distribution and variance homogeneity of residuals was graphically tested with help of a normal probability plot (Crawley 2013). Goodness-of-fit statistics (R^2 -values) for these models were computed with the help of the piecewiseSEM package (Lefcheck 2015). Furthermore, we tested the differences in overall niche overlap regarding habitat use and phenology between spring and autumn season with a Welch Two-sample *t*-test. Based on the available data, we were able to evaluate the existence of stopover niches for 8 species on 3 dimensions: morphology, space, and time.

Results

Morphology

Complete morphometric data of 15 males and 15 females each were available for 8 species (Supplementary Material 2). The results of the PCA are shown in Table 2. When using the original data, the first principal component, explaining 53% of total variance, is negatively correlated with body mass and all other measurements, and therefore, stands for overall size. The second principal component, explaining 17% of total variance, is positively correlated with tail and wing length, whereas the third principal component explaining 16% of total variance is positively correlated with wing pointedness. PC1, PC2, and PC3 are depicted in Figure 1. After correcting for size, we found that the first and the second principal component are

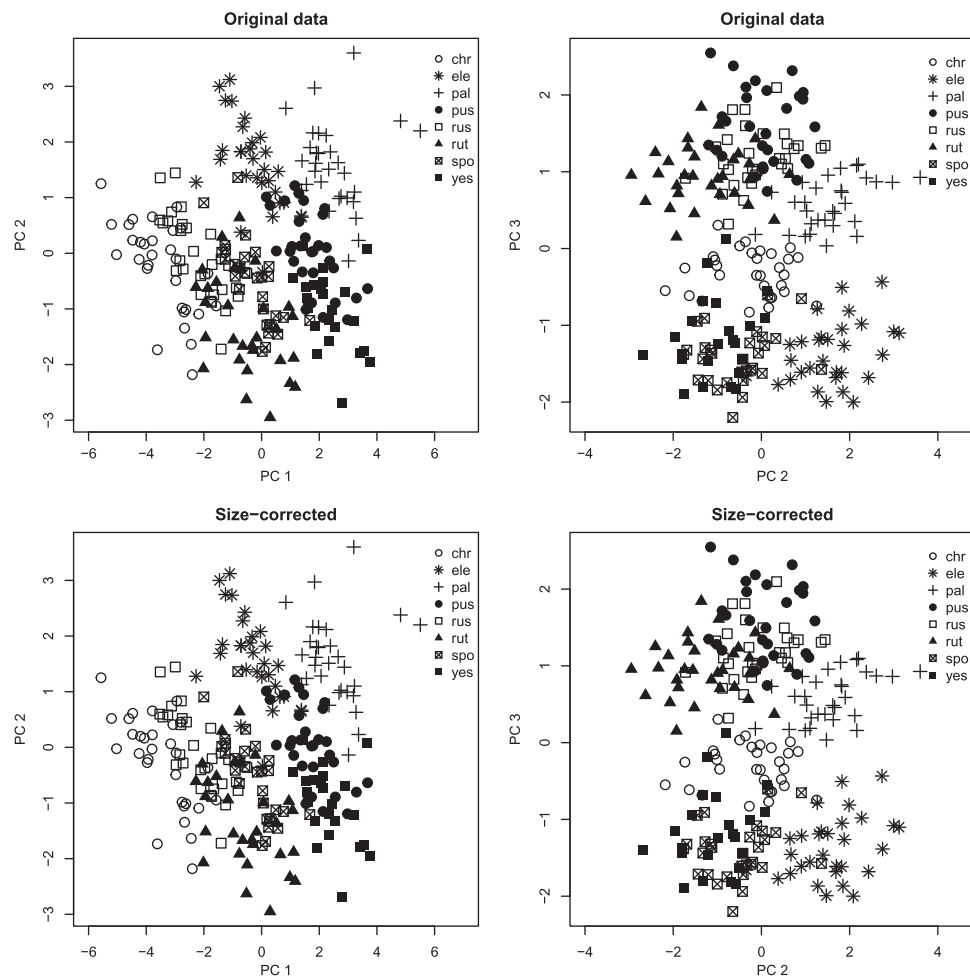


Figure 1. Principal components 1–3 for morphology of 8 bunting species using original data (upper line) and size-corrected data (lower line). The following species were included: Yellow-browed Bunting (chr), Yellow-throated Bunting (ele), Pallas's Reed Bunting (pal), Little Bunting (pus), Rustic Bunting (rus), Chestnut Bunting (rut), Black-faced Bunting (spo) and Ochre-rumped Bunting (yes).

correlated with wing length and wing pointedness, respectively, and explaining 39% and 25% of total variance, whereas the third principal component is negatively correlated with bill and tarsus length explaining 16% of variance. The PCA with the original data explained more of the morphological variance than the PCA based on the size-corrected data.

A similarity index was computed for each of the species pairs. The morphologically most similar species pairs are Pallas's Reed Bunting and Little Bunting with a similarity index of 0.679, the most dissimilar pair are Ochre-rumped Bunting and Yellow-browed Bunting with a similarity index of 0.004 (Figure 2A, Supplementary Material 3). Part of this overall index is the similarity index of bill morphology. The most similar index values were found for Ochre-rumped Bunting and Yellow-throated Bunting; the most unlike pair are Yellow-browed Bunting and Yellow-throated Bunting (Figure 2B, Supplementary Material 3).

Habitat

Trapped buntings were not equally distributed among all habitats, neither in spring ($\chi^2 = 39.588$, $df=5$, $P < 0.001$) nor in autumn ($\chi^2 = 11.833$, $df=5$, $P = 0.037$). Habitat types A–C in the lowlands were most important in years without flood, while the buntings shifted to the habitat types D–E on the terrace in the flood year

2013. This pattern still remains consistent when excluding the superabundant Black-faced Bunting (Supplementary Material 4a). In spring, most buntings were found in the pine plantation (30.4%, Habitat F) and in deciduous trees (22.3%, Habitat D). In autumn, the majority of the birds were trapped in small willow thickets (40.5%, Habitat B) and oak forest with dense understorey (19.5%, Habitat E) —see Supplementary Material 1. Almost all bunting species were found in all kind of habitats (Supplementary Material 4b), with exception of the Ochre-rumped Bunting, in which 80% of the birds were trapped in Habitat type A (reeds). Nevertheless, all species were neither randomly distributed among the habitat types (χ^2 -test, $P < 0.001$), nor among the total traps per habitat (χ^2 -test, $P < 0.05$).

In spring, the 6 studied species can be divided in 3 clusters in terms of their habitat use (Figure 3): (1) Low willow shrubs (pal), (2) species of higher willow shrubs and deciduous forest (ele, pus, rus, spo), and (3) species mainly found in the pine plantation (chr). In autumn, 8 species can be divided into 4 clusters: (1) reed and wetland species (yes), (2) species of low willow thickets (pal, pus, spo), (3) forest species (ele, rus), and (4) species that occur in all habitats (chr, rut).

Habitat use differed significantly between spring and autumn season ($\chi^2 = 115.25$, $df=5$, $P < 0.001$). In spring, 31.8% of all

Table 2. PCA: Factor loadings of the first 3 principal components based on 9 morphological measurements for 8 bunting species

Measurement	Original data			Size-corrected		
	PC1	PC2	PC3	PC1	PC2	PC3
Wing length (Maximum chord)	-0.365	0.362	0.280	0.473	-0.315	-0.216
Length of 8 th primary	-0.346	0.412	0.281	0.481	-0.284	-0.215
Wing pointedness (Kipp-Index)	-0.218	-0.135	0.668	0.087	-0.609	-0.224
Tail length	-0.110	0.629	-0.400	0.360	0.417	-0.211
Tarsus length	-0.321	-0.059	-0.423	0.002	0.409	-0.600
Bill length (Bill to skull)	-0.340	-0.341	-0.178	-0.289	-0.008	-0.629
Bill width (behind nostrils)	-0.369	-0.270	-0.117	-0.376	-0.179	-0.227
Bill height (behind nostrils)	-0.383	-0.295	-0.049	-0.428	-0.276	-0.081
Weight (lean body mass)	-0.431	0.076	-0.100	NA	NA	NA
Proportion of variance	0.545	0.177	0.164	0.391	0.251	0.157
Cumulative proportion of variance	0.545	0.721	0.886	0.391	0.642	0.799

The highest loadings for each component are in bold.

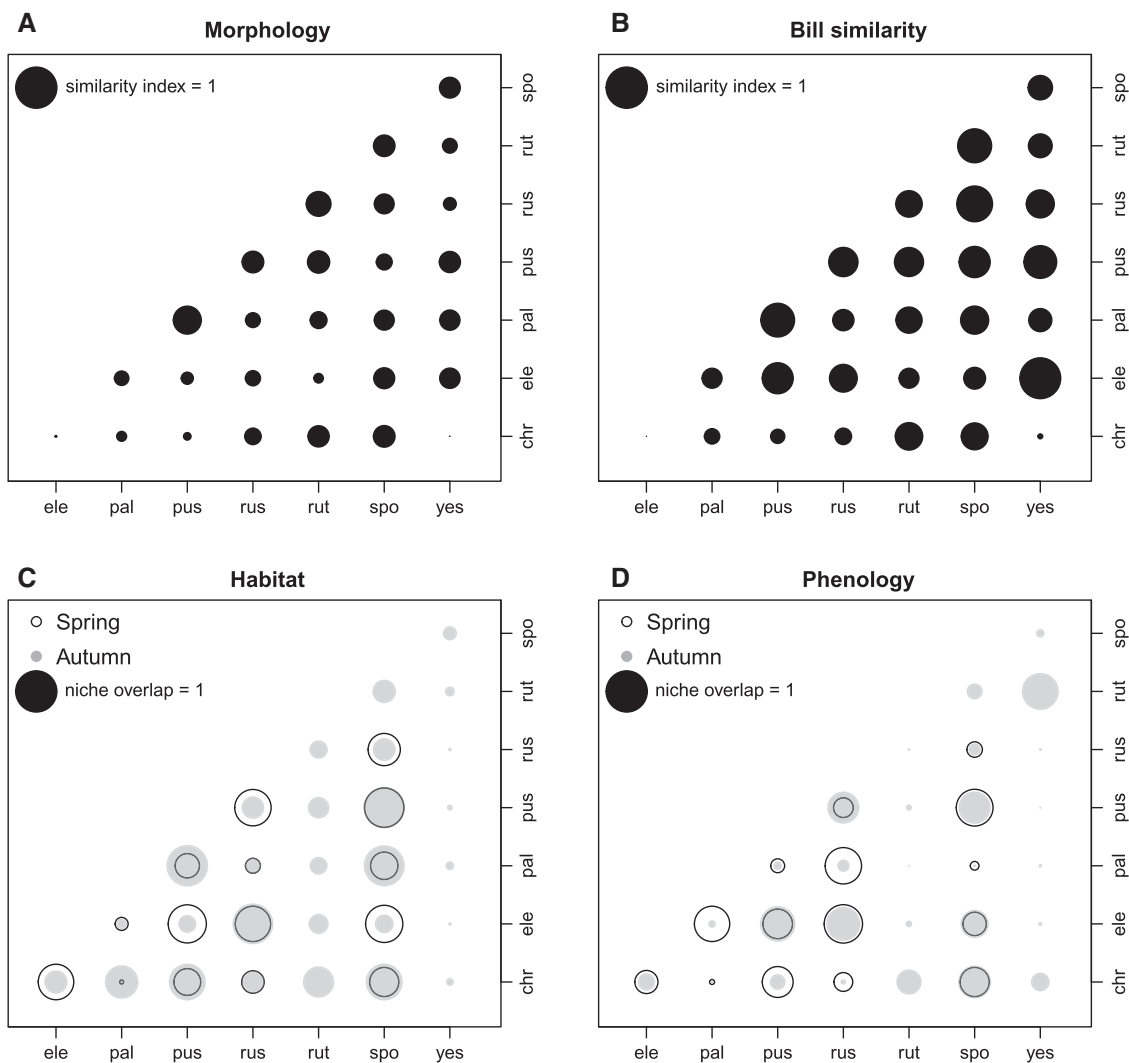


Figure 2. Similarity of 8 bunting species regarding (A) morphology and (B) bill morphology, as well as niche overlap regarding (C) habitat use and (D) phenology. Point size resembles similarity index/niche overlap (range: 0–1). For species abbreviations, see Figure 1.

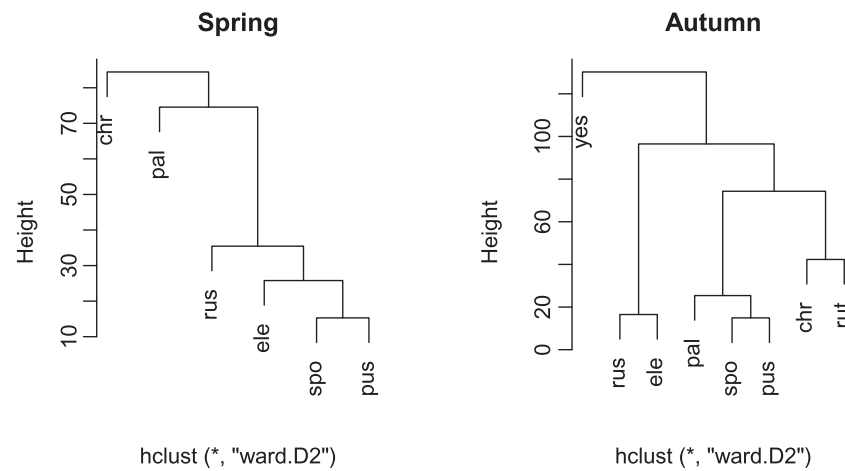


Figure 3. Cluster analysis based on habitat preferences of bunting species during spring (left) and autumn (right) migration. For species abbreviations, see Figure 1.

Table 3. Relative niche breadth of 8 species of buntings regarding habitat use and phenology during spring and autumn

Species	Habitat	Phenology			
		Spring	Autumn	Spring	Autumn
Yellow-browed Bunting	chr	22.7	69.8	18.2	42.7
Yellow-throated Bunting	ele	48.7	52.2	38.3	40.7
Pallas's Reed Bunting	pal	39.6	27.1	24.1	15.1
Little Bunting	pus	62.5	46.0	31.1	29.4
Rustic Bunting	rus	49.3	49.4	26.5	23.4
Chestnut Bunting	rut	NA	54.1	NA	44.1
Black-faced Bunting	spo	84.5	58.3	44.6	38.0
Ochre-rumped Bunting	yes	NA	14.4	NA	29.7

buntings were trapped in the lowlands (Habitats A–C), and 68.2% on the terrace (Habitats D–F). In autumn, it was 61.5% and 36.5%, respectively. This is also true within species: in spring, 41% of all Black-faced Buntings are trapped in lowlands and 59% on the terrace, while in autumn 71% were found in the lowlands and 29% on the terrace. The interspecific differences in habitat use are less pronounced in spring than in autumn.

Relative habitat niche breadth differed among species and between seasons (Table 3). Black-faced Buntings utilized a broader habitat niche during spring than during autumn, whereas Yellow-browed Buntings occupied a narrow niche during spring and a broad one in autumn. Ochre-rumped Buntings utilized the narrowest niche during autumn migration, again highlighting their status as habitat specialists.

The niches of the studied species overlapped during both spring and autumn (Figure 2C, Supplementary Material 3). Highest overlap was found between Black-faced Bunting, Little Bunting, and Pallas's Reed Bunting, as well as between Rustic Bunting and Yellow-throated Bunting. The niches of Chestnut Bunting and Ochre-rumped Bunting during autumn migration showed least overlap with other species.

Phenology

There are pronounced differences in the timing of migration among the 8 studied species (Figure 4A). Spring migration begins with Pallas's Reed Bunting as the earliest species to arrive at the study site,

whereas some Little, Yellow-browed and Black-faced Buntings migrate until the end of May or even the first days of June. Autumn migration starts at the beginning of August in Chestnut and Ochre-rumped Buntings, and ends in the second half of October with Pallas's Reed Bunting being the latest species. The median date of their occurrences at the study site is given in Supplementary Material 5. Significant differences in phenology between years were found for Yellow-throated Bunting ($F_{1,172} = 9.578$, $R^2 = 0.052$, $P = 0.002$) and Pallas's Reed Bunting ($F_{1,51} = 8.149$, $R^2 = 0.138$, $P = 0.006$) during spring migration, and for Ochre-rumped Bunting ($F_{1,49} = 5.462$, $R^2 = 0.100$, $P = 0.024$) as well as Pallas's Reed Bunting ($F_{1,180} = 16.18$, $R^2 = 0.083$, $P < 0.001$) during autumn migration. No significant differences in phenology between years were found for the remaining species (Black-faced Bunting, Chestnut Bunting, Little Bunting, Rustic Bunting, and Yellow-browed Bunting). Phenology for the 5 most common species ($n/\text{year} > 30$) during autumn migrations 2013, 2014, and 2015 is shown in Figure 4B. Occurrence during autumn migration is highly correlated with spring phenology (Figure 5). The final LME to explain the median day of migration reveals significant the variable *northernmost wintering latitude* for spring migration ($R^2 = 0.73$) with more southern wintering species passing late. In autumn, *northernmost breeding latitude* and *migration distance* combined ($R^2 = 0.81$, see Supplementary Material 6) explained passage date ($R_{\text{marg}}^2 = 0.32$ and $R_{\text{marg}}^2 = 0.02$, respectively); with northern breeding birds passing late and species travelling long distances passing early.

Niche overlap

The mean niche overlap in phenology is significantly higher in spring than in autumn ($t = -3.003$, $df = 32.623$, $P = 0.005$), which is also the case for niche overlap in habitat use ($t = -3.302$, $df = 40.491$, $P = 0.002$) (Figure 6, Supplementary Material 3). During spring migration, 6 out of 15 species pairs (40%) show an overlap value in phenology of < 0.5 ($< 50\%$ overlap). Thirty-three percent of all species pairs are well separated regarding bill morphology, and 13% use differential spatial niches. Sixty-six percent of all species pairs were separated on at least 1 dimension. During autumn migration, this is true for 80% (24 of 30 species pairs). In autumn, 63% differ on the temporal dimension, and 37% on the spatial dimension (Figure 7). There is a significant correlation between niche breadth on the spatial and on the temporal dimension (Figure 8). Species

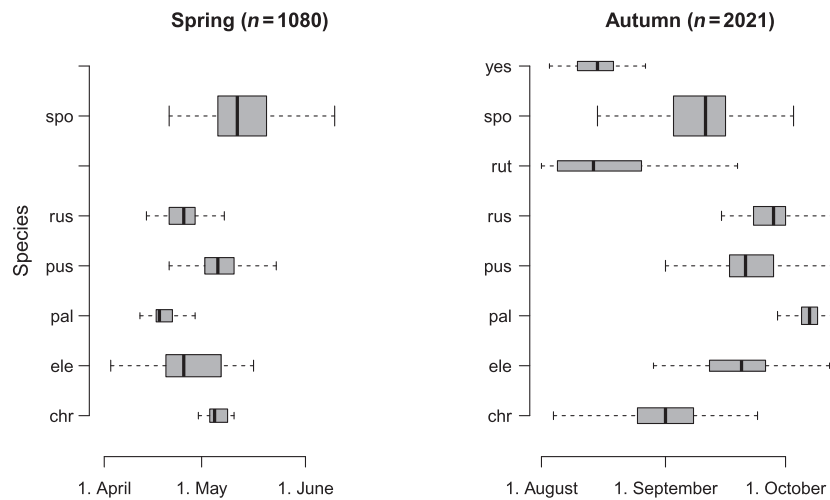


Figure 4A. Phenology during spring (left) and autumn (right) migration. The height of the box resembles sample size. For species abbreviations, see Figure 1.

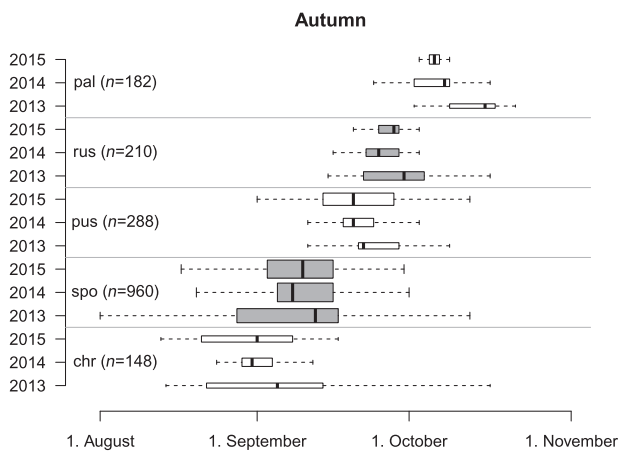


Figure 4B. Inter-annual variability in autumn phenology for the 5 most common bunting species ($n/\text{year} > 30$). The height of the box resembles sample size. Significant differences between years were only found for Pallas’s Reed Bunting. For species abbreviations, see Figure 1.

with a broad temporal niche occur in a broad range of habitats, and vice versa. There are pronounced differences between spring and autumn season within some species, irrespective of sample size.

Discussion

Morphology

Overall size was found to be the most important factor in our PCA, and the size-corrected PCA explained less of the morphological variation among the studied species. Slight but well-pronounced differences in overall size can be an important factor for niche segregation (Alatalo et al. 1986). The observed variability in wing morphology, especially wing pointedness, is likely linked to flight behavior and migration distance (Baldwin et al. 2010). However, these differences might not be relevant regarding niche use when species meet at the stopover site. Some morphologically rather similar species showed high niche overlap in habitat use and phenology as well (for example, Little Bunting and Rustic Bunting). We found that morphologically similar species do not avoid each other on the spatial or temporal scale. Strong differences were only found between those

species situated at the very end of the morphological spectrum, that is, between the smallest species (Ochre-rumped Bunting) and the largest species (Yellow-browed Bunting).

This is also true for bill morphology—only the 2 species with the weakest (Yellow-throated Bunting) and the heaviest bill (Yellow-browed Bunting) showed very low similarity. The extreme low value between the latter 2 species seems to be more a methodological bias (highlighting the ends of the spectrum) rather than a real difference. Since bill morphology was used as a proxy for the feeding structure and the tropic niche, it seems likely, that there are no major differences in diet among the studied species. Buntings form mixed-species flocks, and they were often seen feeding together on the same resources at the study site (personal observations). All species are foraging on seed-bearing plants on or close to the ground. According to Byers et al. (1995), all *Emberiza* buntings switch their diet from invertebrates during the breeding season to a wide range of small seeds during the non-breeding season. In a study by Hasui et al. (2009), niche partitioning among 2 tropical bird species was found only during periods of fruit scarcity. Moore and Yong (1991) found that migrants at stopover sites gained less weight when more birds were around. If food availability is a limiting factor, one would expect high overlap, since migrants are known to use a wide range of available niches under such conditions (Kober and Bairlein 2009). All in all, the studied species are in general not very distinct in morphology, which is likely caused by their close phylogenetic relationship (all 8 species belong to the same genetic clade, even within the genus *Emberiza*, Päckert et al. 2015).

Habitat

Most of the studied species occurred in all available habitat types. In spring, the habitats in the lowlands were found to be of lesser importance for the buntings. This can probably be explained by the fact that they provide less food and shelter before the vegetation period, which usually starts after the majority of the buntings have migrated through. Therefore, it seems possible that there is much stronger competition for suitable habitats during spring migration. Reeds are not of great importance for the studied species during spring migration. However, it has to be noted that the only reed specialist species, the Ochre-rumped Bunting, was not trapped during spring migration in sufficient numbers for an inclusion in the analysis

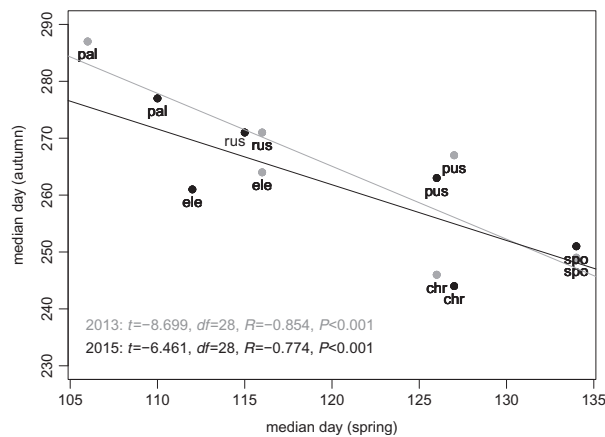


Figure 5. Median dates of occurrence during spring and autumn migration are correlated. For species abbreviations, see Figure 1.

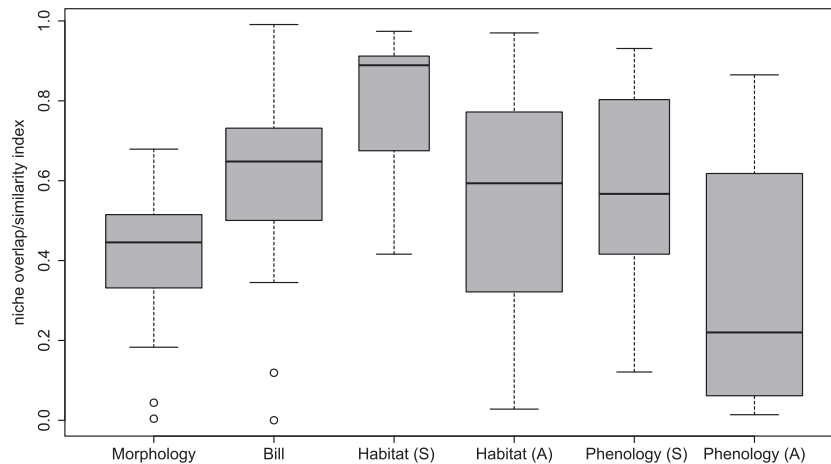


Figure 6. Mean similarity indices and niche overlap values for all species pairs during spring (S) and autumn (A).

(which is also true for Common Reed Bunting *E. schoeniclus*, another reed specialist).

During autumn migration, however, the majority of the individuals and species prefer those habitats in the lowlands, while the forested parts on the river terrace are of lesser importance. This change in habitat use was visible even within species, like for example, in Black-faced Bunting. It can be assumed that the abundance of seed-bearing plants (for example, grasses) is probably higher in the open lowlands than in more forested places. Reed beds and marsh vegetation are known for high arthropod availability in late summer and autumn and their attractiveness to a variety of migrant bird species during this season (Bairlein 1983). The observed patterns of habitat use might therefore reflect food availability or food preferences. Again, high overlap among species would in this case suggest limited resources (Kober and Bairlein 2009; McFarlane Tranquilla et al. 2015). Extreme events, like the flood in 2013, can lead to shifts in habitat use, and might therefore increase competition among species at stopover sites.

Phenology

In comparison with the trophic and spatial dimension, phenology was found to be most important for stopover niche separation

among the studied species. This is especially true for autumn migration, when the mean niche overlap value is much lower than on any other dimension (Figure 6). Differences in phenology between years were found for Yellow-throated Bunting and Pallas's Reed Bunting during spring migration. This might be caused by the delayed start of the ringing season especially in 2016. Yellow-throated and Pallas's Reed Buntings are the earliest to migrate, with some individuals arriving already in March (personal observations), and therefore, the data might not cover the complete migration period. This might also explain the interannual differences in phenology for Pallas's Reed Bunting during autumn migration. In some years, this species is found until November and single birds might overwinter in the area (personal observations). The differences in Ochre-rumped Bunting, however, could be explained with its low sample size—only 11 individuals were trapped in 2015.

All in all, interannual variation does not occur on a large scale, and we assume that the majority of the studied species seems to follow a rather strict schedule during their migration. Similar results were found for buntings during spring migration at a stopover site on the Korean Peninsula, with interannual variation of mean arrival dates by 3 to maximum 10 days (Nam et al. 2011). Two of the studied species are not only migrants but also breed at Muraviivka

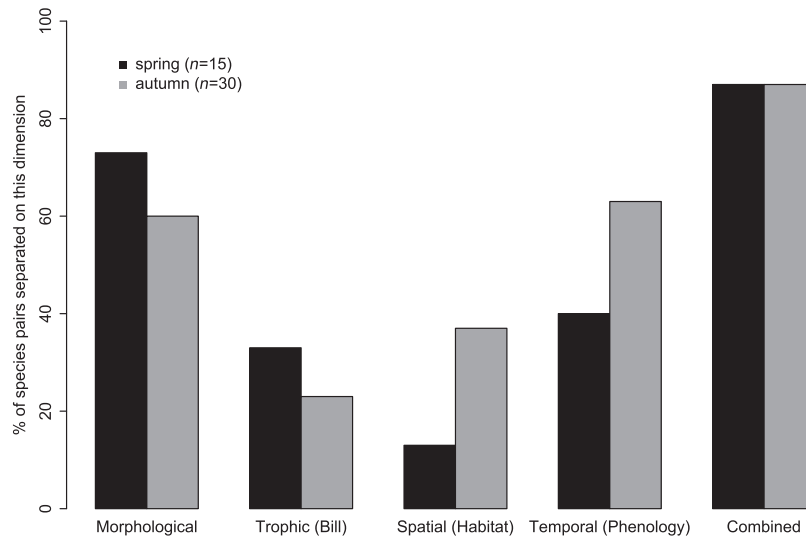


Figure 7. Number of species pairs (in percentage) separated for each niche dimension. A species pair was considered separated if the similarity index or the niche overlap was below 0.5 (<50% overlap). Ninety percent of all species pairs ($n=30$) were separated on at least one dimension.

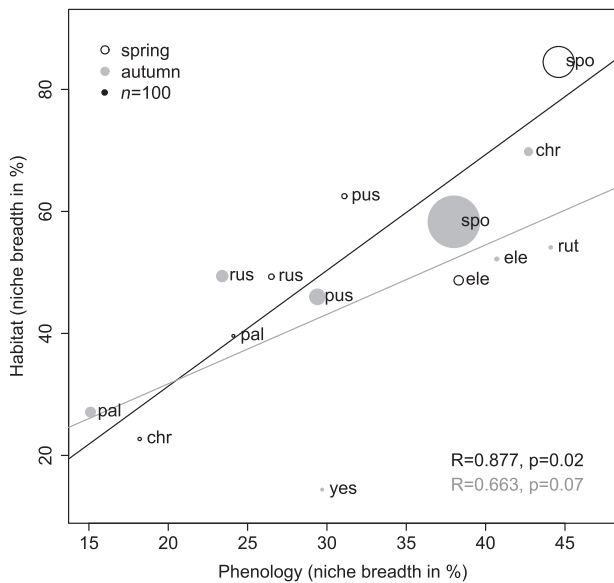


Figure 8. Correlation between relative niche breadth on spatial (habitat) and temporal (phenology) dimension. Point diameter reflects sample size. For species abbreviations, see Figure 1.

Park: Black-faced Bunting and Ochre-rumped Bunting. It is not possible to separate local and transient individuals, unless they are already ringed. Therefore, our analysis of their phenological niche and the median day of occurrence might be biased by local breeding birds. This probably explains the comparatively high relative niche breadth for Black-faced Bunting during spring (Table 3).

The main driver for the observed phenological pattern seems to be the geographic position the birds originate from. This fits to the observation, that migratory Passerines track their preferred climatic conditions (Gómez et al. 2016). Furthermore, migration distance was found to be important during autumn migration. Long-distance migrants are the earliest species to migrate through the study site in autumn, while species with shorter routes occur later. These patterns have been found on stopover sites in North America and Europe as

well (Francis and Cooke 1986; Gatter 2000). Arrival at breeding and stopover sites during spring migration is known to correlate with large-scale climatic indices (Stervander et al. 2005) and depends on temperature en route (Hüppop and Winkel 2006; Tøttrup et al. 2010), conditions on the wintering grounds (Saino et al. 2004; Saino et al. 2007), or both (Tøttrup et al. 2008). In our study, however, the interannual variation was low, and the median differed only by a few days in most cases (Figure 4B). These small-scale differences might be caused by factors listed above, but the general phenological pattern and the chronological order of the studied species was found to be consistent. Precise timing of migration regarding phenology, synchrony, and consistency can affect not only individual fitness, but also population dynamics and gene flow (Bauer et al. 2016). In our study system, with a comparably high number of closely related species, exact timing might be crucial to avoid competition at the stopover site.

Niche overlap

The mean niche overlap was found to be higher in spring than during autumn migration. This might be linked to fewer available habitat (shelter) and food, since bunting migration takes place before the start of the vegetation period (see above). Another reason might be the difference in the length of the migration period (Figure 4A): the majority of the bunting species migrates during spring between mid-April and mid-May (~30 days), whereas the main autumn passage spans from mid-August to mid-October (~60 days). This phenomenon is well known and probably related to strong time pressure to match breeding schedule (Nilsson et al. 2013), causing higher niche overlap on the temporal scale during spring.

Furthermore, we showed that species with a broad temporal niche occur in a broad range of habitats, and that there are pronounced differences between seasons. This is not a bias caused by differences in sample size (Figure 7), but might rather reflect changes in food availability between habitat types within the course of a season. These changes probably force later or earlier arriving individuals to utilize other resources and, therefore, switch the habitat. It is most likely that migrating birds use available resources at stopover

sites opportunistically, instead of tracking their niche (Laube et al. 2015).

Synthesis and limitations

In our study, the most common bunting species showed consistent, well defined and regularly spaced stopover niches along the temporal dimension (Figure 4B; *sensu* Schoener 1974, p. 37). Schoener (1974) states, that “[h]abitat dimensions are important more often than food-type dimensions, which are important more often than temporal dimensions.” In fish communities, food plays the major role, followed by habitat and temporal segregation (Ross 1986). In bats, both spatial, trophic, and temporal dimensions are involved in shaping communities (Patterson et al. 2003). However, these findings might not fit stopover niches of migrating birds, which are obviously more characterized on a temporal scale. Long-distance migrants are known to be less flexible in their phenology compared with short-distance migrants (Moussus et al. 2011), and all of the species included in our study have long or very long migration routes (mean distance of mean breeding and wintering range of more than 12 latitudes, Supplementary Material 2).

In this work, we investigated interspecific niche segregation. However, intraspecific differences in niche utilization might occur between sexes—which was shown for highly dimorphic woodpeckers (Selander 1966; Williams 1980) and warblers (Franzreb 1983; Petit et al. 1990), but was not found in Blue Tits *Cyanistes caeruleus* (Przybylo and Merilä 2000). Furthermore, niche breadth was found to be positively correlated with sexual size dimorphism (Brändle et al. 2002). On the other hand, even in species with strong sexual differences in bill morphology there can be no dietary specialization (Franks et al. 2013). On top of that, there could be competition not only within the different species of buntings, but also with other seed-eating and shrub- or ground-dwelling birds. However, in this work we focused on relative niches within the group, and not on the absolute niche.

Acknowledgments

The manuscript was improved by comments of Fumin Lei and Zhi-Jun Yia and 2 anonymous reviewers as well as Ramona Heim, Susanne Jähmig, Johannes Kamp, Martha Maria Sander, Arne Schlegelmilch, and Melanie Dammhahn plus the Animal Ecology working group at the University of Potsdam.

Funding

The work of the Amur Bird Project at Muraviovka Park was supported by the Förderkreis Allgemeine Naturkunde (Biologie) e.V., German Ornithologists' Society (DO-G e.V.), NABU Regionalverband Erzgebirge e.V., The Sound Approach, Mohamed bin Zayed Species Conservation Fund, British Ornithologists' Union, Oriental Bird Club, ProRing e.V., Rotary Club Potsdam, Ornithologischer Verein zu Leipzig e.V., Carl Zeiss Sports Optics as well as private donors and supporters.

Author contributions

W.H. has designed the study, collected the data, run the analysis, and wrote the manuscript. J.A.E. and F.B. have designed data analysis and provided literature. F.B. has written parts of the manuscript.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>

References

- Ai D, Chu C, Ellwood MDF, Hou R, Wang G, 2013. Migration and niche partitioning simultaneously increase species richness and rarity. *Ecol Modell* 258:33–39.
- Alatalo RV, Gustafsson L, Lundberg A, 1986. Interspecific competition and niche changes in tits (*Parus* spp.): evaluation of nonexperimental data. *Am Nat* 127:819–834.
- Albrecht M, Gotelli NJ, 2001. Spatial and temporal niche partitioning in grassland ants. *Oecologia* 126:134–141.
- Bairlein F, 1981. Ökosystemanalyse der Rastplätze von Zugvögeln: Beschreibung und Deutung der Verteilungsmuster von ziehenden Kleinvögeln in verschiedenen Biotopen der Stationen des “Metttau-Reit-Illmitz-Programmes”. *Ökologie der Vögel* 3:7–137.
- Bairlein F, 1983. Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. *Ornis Scandinavica* 14:239–245.
- Bairlein F, 1992. Morphology-habitat relationships in migrating songbirds. In: Hagan JM III, Johnston DW, editors. *Ecology and Conservation of Neotropical Migratory Landbirds*. Washington (DC): Smithsonian Institution Scholarly Press, 354–368.
- Bairlein F, 2016. Migratory birds under threat. *Science* 354:547–548.
- Bairlein F, Norris DR, Nagel R, Bulte M, Voigt CC et al., 2012. Cross-hemisphere migration of a 25 g songbird. *Biol Lett* 8:505–507.
- Baldwin MW, Winkler H, Organ CL, Helm B, 2010. Wing pointedness associated with migratory distance in common-garden and comparative studies of stonechats *Saxicola torquata*. *J Evol Biol* 23:1050–1063.
- Bauer S, Lisovski S, Hahn S, 2016. Timing is crucial for consequences of migratory connectivity. *Oikos* 125:605–612.
- Bensusan KJ, Shorrocks B, Hamer KC, 2011. Impacts of passage migrant songbirds on behaviour and habitat use of resident Sardinian warblers *Sylvia melanocephala* in Gibraltar. *Ibis* 153:616–621.
- BirdLife International 2017. *IUCN Red List for Birds*. [cited 2017 November 21] Available from <http://www.birdlife.org>.
- Bocher P, Kojadinovic J, Delaporte P, Rousseau P, Dupuy C et al., 2014. Trophic resource partitioning within a shorebird community feeding on intertidal mudflat habitats. *J Sea Res* 92:115–124.
- Bolshakov CV, Chernetsov N, Mukhin A, Bulyuk VN, Kosarev V et al., 2007. Time of nocturnal departures in European robins *Erithacus rubecula* in relation to celestial cues, season, stopover duration and fat stores. *Anim Behav* 74:855–865.
- Brändle M, Prinzing A, Pfeifer R, Brandl R, 2002. Dietary niche breadth for Central European birds: correlations with species-specific traits. *Evol Ecol Res* 4:643–657.
- Burger J, Carlucci SA, Jeitner CW, Niles L, 2007. Habitat choice, disturbance, and management of foraging shorebirds and gulls at a migratory stopover. *J Coast Res* 28:1159–1166.
- Byers C, Olsson U, Curson J, 1995. *Buntings and Sparrows*. Sussex: Pica Press.
- Carothers JH, Jaksic FM, 1984. Time as a niche difference: the role of interference competition. *Oikos* 42:403–406.
- Castro-Arellano I, Lacher TE, 2009. Temporal niche segregation in two rodent assemblages of subtropical Mexico. *J Trop Ecol* 25:593–603.
- Chase JM, 2011. Ecological niche theory. In: Scheiner S, Willing M, editors. *The Theory of Ecology*. Chicago: The University of Chicago Press.
- Choi C-Y, Battley PF, Potter MA, Ma Z, Melville DS et al., 2017. How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species. *Auk* 134:76–91.
- Crawley MJ, 2013. *The R Book*. 2nd edn. Chichester: Wiley.
- Dammhahn M, Rakotondramanana CF, Goodman SM, 2015. Coexistence of morphologically similar bats (Vespertilionidae) on Madagascar: stable isotopes reveal fine-grained niche differentiation among cryptic species. *J Trop Ecol* 31:153–164.
- Davis CM, Smith LM, 2001. Foraging strategies and niche dynamics of coexisting shorebirds at stopover sites in the southern great plains. *Auk* 118:484–495.
- Dennis AB, Hellberg ME, 2010. Ecological partitioning among parapatric cryptic species. *Mol Ecol* 19:3206–3225.

- Eck S, Fiebig J, Fiedler W, Heynen I, Nicolai B et al., 2011. Vögel vermessen/-measuring birds. Deutsche Ornithologen-Gesellschaft, Christ Media Natur, Minden.
- Edenius L, Choi C-Y, Heim W, Jaakkonen T, De Jong A et al., 2017. The next common and widespread bunting to go? Global population decline in the rustic bunting *Emberiza rustica*. *Bird Conserv Int* 27:35–44.
- Francis CM, Cooke F, 1986. Differential timing of spring migration in wood warblers *Parulinae*. *Auk* 103:548–556
- Franks SE, Fernandez G, Hodkinson DJ, Kyser TK, Lank DB, 2013. The long and the short of it: no dietary specialisation between male and female western sandpipers despite strong bill size dimorphism. *PLoS ONE* 8:e79835.
- Franzreb KE, 1983. Intersexual habitat partitioning in yellow-rumped warblers during the breeding season. *Wilson Bull* 95:581–590.
- Gatter W, 2000. *Vogelzug und Vogelbestände in Mitteleuropa. 30 Jahre Beobachtung des Tagzugs am Randecker Maar*. Wiebelsheim: AULA-Verlag.
- Gerrish GA, Morin JG, Rivers TJ, Patrawala Z, 2009. Darkness as an ecological resource: the role of light in partitioning the nocturnal niche. *Oecologia* 160:525–536.
- Gilbert B, Srivastava DS, Kirby KR, 2008. Niche partitioning at multiple scales facilitates coexistence among mosquito larvae. *Oikos* 117:944–950.
- Gómez C, Tenorio EA, Montoya P, Cadena CD, 2016. Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers *Parulidae*. *Proc R Soc B Biol Sci* 283:e20152458.
- Grinnell J, 1917. The niche-relationships of the California thrasher. *Auk* 34: 427–433.
- Haegeman B, Loreau M, 2011. A mathematical synthesis of niche and neutral theories in community ecology. *J Theor Biol* 269:150–165.
- Hagen CA, Pitman JC, Robel RJ, Loughin TM, Applegate RD, 2007. Niche partitioning by lesser prairie-chicken *Tympanuchus pallidicinctus* and ring-necked pheasant *Phasianus colchicus* in Southwestern Kansas. *Wildl Biol* 13:34–41.
- Hasui É, Gomes VSDM, Kiefer MC, Tamashiro J, Silva WR, 2009. Spatial and seasonal variation in niche partitioning between blue manakin *Chiroxiphia caudata* and greenish schiffornis *Schiffornis virescens* in southeastern Brazil. *Stud Neotrop Fauna E* 44:149–159.
- Hayward MW, Slotow R, 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South Afr J Wildl* 39: 109–125.
- Heim W, Smirenski SM, 2013. The Amur bird project at Muraviovka Park in Far East Russia. *BirdingASIA* 19:31–33.
- Heim W, Smirenski SM, Siegmund A, Eidam F, 2012. Results of an autumnal bird ringing project at Muraviovka Park (Amur Region) in 2011. *Avian Ecol Behav* 21:27–40.
- Henry CS, Wells MM, 2010. Acoustic niche partitioning in two cryptic sibling species of *Chrysoperla* green lacewings that must duet before mating. *Anim Behav* 80:991–1003.
- Hinke JET, Polito MJ, Goebel ME, Jarvis S, Reiss CS et al., 2015. Spatial and isotopic niche partitioning during winter in chinstrap and Adeline penguins from the South Shetland Islands. *Ecosphere* 6:1–32.
- Hüppop O, Winkel W, 2006. Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migration routes. *J Ornithol* 147:344–353.
- Jędrzejewski W, Jędrzejewska B, Szymura A, 1989. Food niche overlaps in a winter community of predators in the Białowieża Primeval Forest, Poland. *Acta Theriologica* 34:487–496.
- Jing K, Ma Z, Li B, Li J, Chen J, 2007. Foraging strategies involved in habitat use of shorebirds at the intertidal area of Chongming Dongtan, China. *Ecol Res* 22:559–570.
- Joseph L, Stockwell D, 2000. Temperature-based models of the migration of Swainson's flycatcher *Myiarchus swainsoni* across South America: a new use for museum specimens of migratory birds. *Proc Acad Nat Sci Phila* 150: 293–300.
- Kaboli M, Aliabadian M, Prodon R, 2007. Niche segregation, behavioural differences, and relation to morphology in two Iranian syntopic wheatears: the Northern Wheatear *Oenanthe oenanthe libanotica* and Mourning Wheatear *O. lugens persica*. *Vie et Milieu- Life and Environment* 57: 137–148.
- Kamp J, Oppel S, Ananin AA, Durnev YA, Gashev SN et al., 2015. Global population collapse in a superabundant migratory bird and illegal trapping in China. *Conserv Biol* 29:1684–1694.
- Klaassen M, 1996. Metabolic constraints on long-distance migration in birds. *J Exp Biol* 199:57–64.
- Knudsen E, Lindén A, Ergon T, Jonzén N, Vik JO et al., 2007. Characterizing bird migration phenology using data from standardized monitoring at bird observatories. *Clim Res* 35:59–77.
- Kober K, Bairlein F, 2009. Habitat choice and niche characteristics under poor food conditions: a study on migratory nearctic shorebirds in the intertidal flats of Brazil. *Ardea* 97:31–42.
- Kosiński Z, Winięcki A, 2004. Nest-site selection and niche partitioning among the great spotted woodpecker *Dendrocopos major* and middle spotted woodpecker *Dendrocopos medius* in riverine forest of Central Europe. *Ornis Fennica* 81:145–156.
- Kronfeld-Schor N, Dayan T, 2003. Partitioning of time as an ecological resource. *Annu Rev Ecol Evol Syst* 34:153–181.
- Laube I, Graham CH, Böhning-Gaese K, 2015. Niche availability in space and time: migration in Sylvia warblers. *J Biogeogr* 42:1896–1906.
- Laughlin AJ, Karsai I, Alsop FJ, 2013. Habitat partitioning and niche overlap of two forest thrushes in the Southern Appalachian spruce - fir forests. *Condor* 115:394–402.
- Lefcheck JS, 2015. piecewiseSEM: piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods Ecol Evol* 7:573–579.
- Leibold MA, 2008. Return of the niche. *Nature* 454:3–4.
- Leibold MA, McPeck MA, 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399–1410.
- Martinez-Meyer E, Peterson AT, Navarro-Sigüenza AG, 2004. Evolution of seasonal ecological niches in the *Passerina* buntings (Aves: Cardinalidae). *Proc R Soc B Biol Sci* 271:1151–1157.
- McFarlane Tranquilla L, Montevecchi WA, Hedd A, Regular PM, Robertson GJ et al., 2015. Ecological segregation among thick-billed murres *Uria lomvia* and common murres *Uria aalge* in the Northwest Atlantic persists through the nonbreeding season. *Can J Zool* 93:447–460.
- Menz MHM, Arlettaz R, 2012. The precipitous decline of the ortolan bunting *Emberiza hortulana*: time to build on scientific evidence to inform conservation management. *Oryx* 46:122–129.
- Moore FR, Yong W, 1991. Evidence of food-based competition among passerine migrants during stopover. *Behav Ecol Sociobiol* 28:85–90.
- Mouillot D, 2007. Niche-assembly vs. dispersal-assembly rules in coastal fish metacommunities: implications for management of biodiversity in brackish lagoons. *J Appl Ecol* 44:760–767.
- Moussus J-P, Jiguet F, Julliard R, 2011. Which are the phenologically flexible species? A case study with common passerine birds. *Oikos* 120:991–998.
- Munoz F, Ramesh BR, Couteron P, 2014. How do habitat filtering and niche conservatism affect community composition at different taxonomic resolutions? *Ecology* 95:2179–2191.
- Nakazawa Y, Peterson AT, Martinez-Meyer E, Navarro-Sigüenza AG, 2004. Seasonal niches of nearctic-neotropical migratory birds: implications for the evolution of migration. *Auk* 121:610–618.
- Nam HY, Choi CY, Park JG, Hong GP, Won IJ et al., 2011. Protandrous migration and variation in morphological characters in *Emberiza* buntings at an East Asian stopover site. *Ibis* 153:494–501.
- Newton I, 2004. Population limitation in migrants. *Ibis* 146:197–226.
- Nilsson C, Klaassen RHG, Alerstam T, 2013. Differences in speed and duration of bird migration between spring and autumn. *Am Nat* 181:837–845.
- Orben RA, Irons DB, Paredes R, Roby DD, Phillips RA et al., 2015. North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations. *J Biogeogr* 42:401–412.
- Päckert M, Sun Y-H, Strutzenberger P, Valchuk O, Tietze DT et al., 2015. Phylogenetic relationships of endemic bunting species (Aves, Passeriformes, Emberizidae, *Emberiza koslowi*) from the eastern Qinghai-Tibet Plateau. *Vertebr Zool* 65:135–150.

- Papes M, Peterson AT, Powell GVN, 2012. Vegetation dynamics and avian seasonal migration: clues from remotely sensed vegetation indices and ecological niche modelling. *J Biogeogr* 39:652–664.
- Patterson BD, Willig MR, Stevens RD, 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. *Bat ecology* 9:536–557.
- Petit LJ, Petit DR, Petit KE, Fleming WJ, 1990. Intersexual and temporal variation in foraging ecology of prothonotary warblers during the Breeding Season. *Auk* 107:133–145.
- Pianka ER, 1973. The structure of lizard communities. *Annu Rev Ecol Evol Syst* 4:53–74.
- Pianka ER, 1981. Competition and niche theory. In: May RM, editor. *Theoretical Ecology Principles and Applications*. Oxford: Oxford University Press.
- Piet GJ, Pet JS, Guruge WAHP, Vijverberg J, Van Densen WLT, 1999. Resource partitioning along three niche dimensions in a size-structured tropical fish. *Can J Fish Aquat Sci* 56:1241–1254.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team 2016. *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1–125.
- Popielarz PA, Neal ZP, 2007. The niche as a theoretical tool. *Annu Rev Sociol* 33:65–84.
- Przybylo R, Merilä J, 2000. Intersexual niche differentiation in the blue tit *Parus caeruleus*. *Biol J Linn Soc* 69:233–244.
- Quillfeldt P, Chel Y, Masello JF, Delord K, McGill RAR et al. 2015. Half a world apart? Overlap in nonbreeding distributions of Atlantic and Indian Ocean thin-billed Prions. *PLoS ONE* 10:1–18.
- Quillfeldt P, Masello JF, Navarro J, Phillips RA, 2013. Year-round distribution suggests spatial segregation of two small petrel species in the South Atlantic. *J Biogeogr* 40:430–441.
- R Core Team 2016. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Ricklefs RE, Cox GW, 1977. Morphological similarity and ecological overlap among passerine birds on St. Kitts, British West Indies. *Oikos* 29: 60–66.
- Ross ST, 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 2:352–388.
- Saino N, Rubolini D, Jonzén N, Ergon T, Montemaggiore A et al., 2007. Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. *Clim Res* 35:123–134.
- Saino N, Szep T, Romano M, Rubolini D, Spina F et al., 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* 7:21–25.
- Salewski V, Jones P, 2006. Palearctic passerines in Afrotropical environments: a review. *J Ornithol* 147:192–201.
- Schmaljohann H, Becker PJJ, Karaardic H, Liechti F, Naef-Daenzer B et al., 2011. Nocturnal exploratory flights, departure time, and direction in a migratory songbird. *J Ornithol* 152:439–452.
- Schmaljohann H, Buchmann M, Fox JW, Bairlein F, 2012. Tracking migration routes and the annual cycle of a trans-Saharan songbird migrant. *Behav Ecol Sociobiol* 66:915–922.
- Schmaljohann H, Meier C, Arlt D, Bairlein F, Van Oosten H et al., 2016. Proximate causes of avian protandry differ between subspecies with contrasting migration challenges. *Behav Ecol* 27:321–331.
- Schoener TW, 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 19:189–213.
- Schoener TW, 1974. Research on how similar species divide resources helps. *Science* 185:27–39.
- Selander RK, 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113–151.
- Shao S, Quan Q, Cai T, Song G, Qu Y et al., 2016. Evolution of body morphology and beak shape revealed by a morphometric analysis of 14 Paridae species. *Front Zool* 13:30.
- Sokolova GV, 2015. Analyzing the Amur River water regime for the period preceding the catastrophic flood in 2013. *Russ Meteorol Hydrol* 40:477–479.
- Stervander M, Lindström A, Jonzen N, Andersson A, 2005. Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. *J Avian Biol* 36:210–221.
- Tøttrup AP, Thorup K, Rainio K, Yosef R, Lehikoinen E, 2008. Avian migrants adjust migration in response to environmental conditions en route. *Biol Lett* 4:685–688.
- Tøttrup AP, Rainio K, Coppack T, Lehikoinen E, Rahbek C, 2010. Local temperature fine-tunes the timing of spring migration in birds. *ntegr Comp Biol* 50:293–304.
- Vergnon R, Dulvy NK, Freddleton RP, 2009. Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecol Lett* 12: 1079–1090.
- Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP et al., 2003. Costs of migration in free-flying songbirds. *Nature* 423:704.
- Williams JB, 1980. Intersexual niche partitioning in downy woodpeckers. *The Wilson Bull* 92:439–451.
- Wilson RP, 2010. Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Funct Ecol* 24:646–657.
- Winkler H, Leisler B, 1992. On the ecomorphology of migrants. *Ibis* 134: 21–28.
- Yong DL, Liu Y, Low BW, Española CP, Choi C-Y et al., 2015. Migratory songbirds in the East Asian-Australasian flyway: a review from a conservation perspective. *Bird Conserv Int* 25:1–37.
- Yosef R, Tryjanowski P, 2002. Spring migration ecology of Cretzschmar's bunting *Emberiza Caesia* through Elat, Israel. *Isr J Zool* 48:150–153.
- Young HS, McCauley DJ, Dirzo R, Dunbar RD, Shaffer SA, 2010. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. *Mar Ecol Prog Ser* 416:285–294.
- Zhang J, 2016. *spaa: Species Association Analysis*. R package version 0.2.2.