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RESEARCH PAPER

Detectability of birds under different sampling efforts and during the breeding season: a case study from Central Europe

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Abstract. During the years 2019 and 2020, I conducted a bird survey transect in the Bohemian Forest. I did not record any changes in habitat structure or weather conditions between the two years. The two surveys differed in sampling effort, which was significantly lower in 2020 (n = 5 visits) than 2019 (n = 14 visits). I found that sampling effort affected the assessment of avian community diversity but did not affect the total number of individuals recorded. I also recorded a similar pattern in the cumulative number of species between the two breeding seasons, but 80% of species were recorded ten days earlier with the higher sampling effort. In the year with the lower sampling effort, I recorded fewer species than in the year with higher sampling effort. In both study periods, avian community diversity peaked during May and June. These results suggest that even a sampling effort three times lower is still sufficient to detect most species if the minimal number of visits are conducted. The pattern of detectability during the breeding season differed significantly among species. Most species (n = 24) showed a decreasing linear detectability throughout the summer months (e.g. Turdidae or Muscicapidae), most probably due to their breeding activities. In two species (willow tit *Poecile montanus* and European goldfinch *Carduelis carduelis*), this linear relationship was reversed, probably due to singing of young birds from the previous breeding season and the effect of the autumn equinox on birdsong activity. Many species (n = 21) did not show any trend and the rest, mainly migratory species, showed non-linear relationships with the peak in the middle of the breeding season. The differences in trends of detectability (i.e. song activity) among bird species are therefore directly linked with their life history.

Key words: bird community, detection, intra-seasonal changes, field effort, song activity

Introduction

Bird monitoring is widely used to understand bird habitat requirements, population changes and the occurrence of each species to assess their geographical ranges (Rosenstock et al. 2002). However, the use of appropriate methods for bird surveys is an often discussed topic because the results can be affected by biases caused by insufficient sampling effort (Pendleton 1995, Neave et al. 1997, Walther & Martin 2001, Thompson 2002, Watson 2017). These biases can be the result of different detectability among species caused by, for example, a positive correlation between the detectability of species and their abundance (Sliwinski et al. 2016). Therefore, insufficient sampling effort may lead to the underestimation of rare species and authors suggest using species with the lowest detectability to calculate the number of visits needed to detect the majority of species in an avian community. Simultaneously, the detectability of a species can be determined by the loudness of its song, reproductive activities during the breeding season, and weather conditions (Slagsvold 1977, O'Connor & Hicks 1980). Solutions that may at least partially mitigate the above-mentioned shortcomings of bird surveys include considering distance sampling method, appropriate timing of the bird survey, and an appropriate number of visits (Buckland et al. 2008).

An appropriate number of visits may be crucial to get a realistic picture of bird community structure. Sampling effort may considerably affect some population characteristics such as species richness (Walther & Martin 2001) or number of detected individuals per species (Rosenstock et al. 2002). In general, it is useful to calculate the detectability of each species (McArdle 1990) and then simulate the minimal number of visits needed for detection of the species with the lowest detectability (Sliwinski et al. 2016).

During the breeding season, the song activity of many species is influenced by their breeding activities, primarily, the peak in song activity of a species corresponds with the date of egg laying, and egg laying terminates song activity (Slagsvold 1977). However, other factors may also play important roles. For example, the song activity of adult birds may increase again during the autumn due to the similar length of day and night around the spring and autumn equinoxes (Brenowitz et al. 1991, Nottebohm 2004). Meanwhile, young birds from the preceding breeding season start to sing, possibly increasing species detectability during autumn (Marler & Slabbekoorn 2004). Whether the species is migratory or resident is another important factor which directly affects the numbers of individuals detected. Therefore, the detectability during the breeding season may differ considerably among different bird species.

In this study, I compared the results of two bird surveys in the same area in different years using different levels of sampling effort and assessed differences among bird species' detectability trends during the breeding seasons. More specifically, I asked if the decreased sampling effort would lead to 1) decreased recorded avian community diversity, 2) decreased recorded number of species or 3) decreased recorded number of individuals. As a separate topic, 4) I compared detectability trends of the species during the breeding season (from data pooled over both breeding seasons) and discuss possible explanations for different patterns among the species.

Methods

Study area

The study took place within the Bohemian Forest National Park in Southern Bohemia (Czech Republic, Fig. 1). The transect was located along the road from Přední Zvonková to the Austrian border (border crossing Zvonková/Schöneben, middle point: 48.7208764 N, 13.9823594 E) at an elevational of 780-860 m a.s.l. This road represents the south-eastern border of the National Park. The road is lined in a mosaic of pasture, moist mountain meadows, scattered forest patches dominated mainly by Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*), and open forests dominated by a mix of European ash (*Fraxinus excelsior*), sycamore maple (*Acer pseudoplatanus*), Norway maple (*Acer platanoides*), mountain-ash (*Sorbus aucuparia*) and common oak (*Quercus robur*). Within the transect, the road crosses several small streams surrounded by different forest types, such as a mix of European white birch (*Betula pendula*) and Eurasian aspen (*Populus tremula*) with scattered willows (*Salix* sp.). The survey transect begins in the small village of Přední Zvonková and transitions to a semi-natural landscape that is not inhabited by humans and represents a semi-open habitat. The largest forest patch surrounds the road near the border crossing. According to landcover database Corine 2018 (Buchhorn et al. 2019), the dominant habitat within the transect buffer (length 3.7 km, area 115 ha) is natural grassland (34.8%), followed by pasture (22.8%), land under cultivation with significant areas of natural vegetation (21.6%), coniferous forests (11.5%) and transitional woodland-shrub (9.3%). The area is located outside any rapidly developing areas and no changes in vegetation structure were recorded between the study years. Mean annual precipitation according to www.worldweatheronline.com database reaches 690 mm. Mean monthly temperature (Wilcoxon matched pairs test, $Z = 0.73$, $P = 0.465$) and monthly aggregate rainfall (Wilcoxon matched pairs test, $Z = 0.93$, $P = 0.345$) did not change between the years 2019 and 2020.

Field data collection

The dataset for this study is a subset of a survey on the effect of road reconstruction on the bird and mammal communities, conducted by the author to assess priorities for conservation within the area. The transect visits each year covered a five-month period from April to August. However, sampling effort differed between the two years (2019 and 2020). In 2019, I conducted 14 transect surveys (in April – 2,

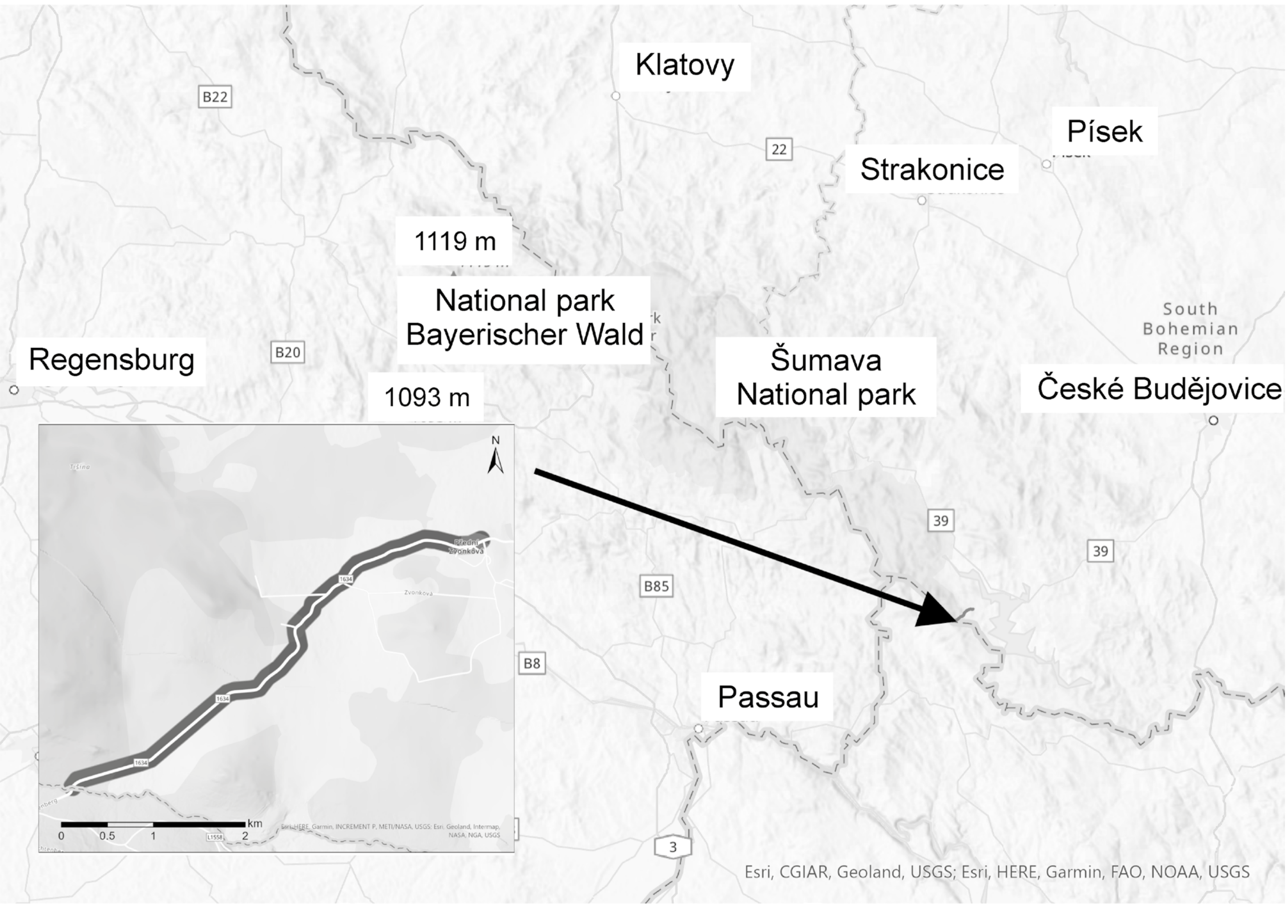

Fig. 1. Location of transect with a buffer of radius 50 m from Přední Zvonková to the Austrian border and study area location within Southern Bohemia. The map was created using ArcGIS Pro software with world topographic basemap (ESRI).

May – 3, June – 3, July – 3 and August – 3) and in the year 2020 I performed only one visit per month (n = 5). Each transect visit was conducted on dry days between 5:30 and 9:00 am, depending on sunrise time.

During the transect surveys, I walked slowly down the road and recorded all individuals heard and/or seen up to 50 m on either side of the road covering an area of 0.37 km^2, as recommended by Buckland (Buckland 2006). Buckland et al. (2008) pointed out that transects along roads are not appropriate due to disturbance from moving vehicles. However, this is not the case in my study area, where median frequency during the surveys did not exceed 15 vehicles per hour (own unpublished data). The starting points (village Přední Zvonková or border crossing Zvonková/Schöneben) were randomly changed. Most records (> 90%) were territorial displays of birds detected aurally. The total abundance of each species in the transect per visit was assessed based on simultaneous song and visual detections of individuals (Bibby et al. 2000). I recorded the numbers of adult individuals, spring flocks of adult birds, and juvenile individuals separately. Juveniles were detected either with parents as newly fledged (June-July) or in flocks (August). When counting the number of adult birds, I multiplied the number of recorded singing males by two to account for the presence of their females. I excluded records of winter visitors (great grey shrike *Lanius excubitor*, brambling *Fringilla montifringilla*) and migrants (European pied flycatcher *Ficedula hypoleuca*), which were occasionally recorded in April, from further analyses. For each visit I calculated a Shannon-Wiener index of diversity (Shannon 1948) after following formula: $H' = -\sum pi * \ln(pi)$, where pi was a proportion of i-species in the bird community based on its abundance.

Statistical analyses

Cumulative plots were created using non-linear estimation function. Between-year differences in numbers of species, total numbers of individuals, numbers of individuals within a category of observation type (adult individuals, flocks of adults and juveniles) and diversity index for each month were analysed using a Wilcoxon matched pairs test. Before these analyses, I calculated monthly means for 2019 with more visits (3-4) per month. For 2020, I used a single value for each month. Relationships between species abundance and day in the season based on

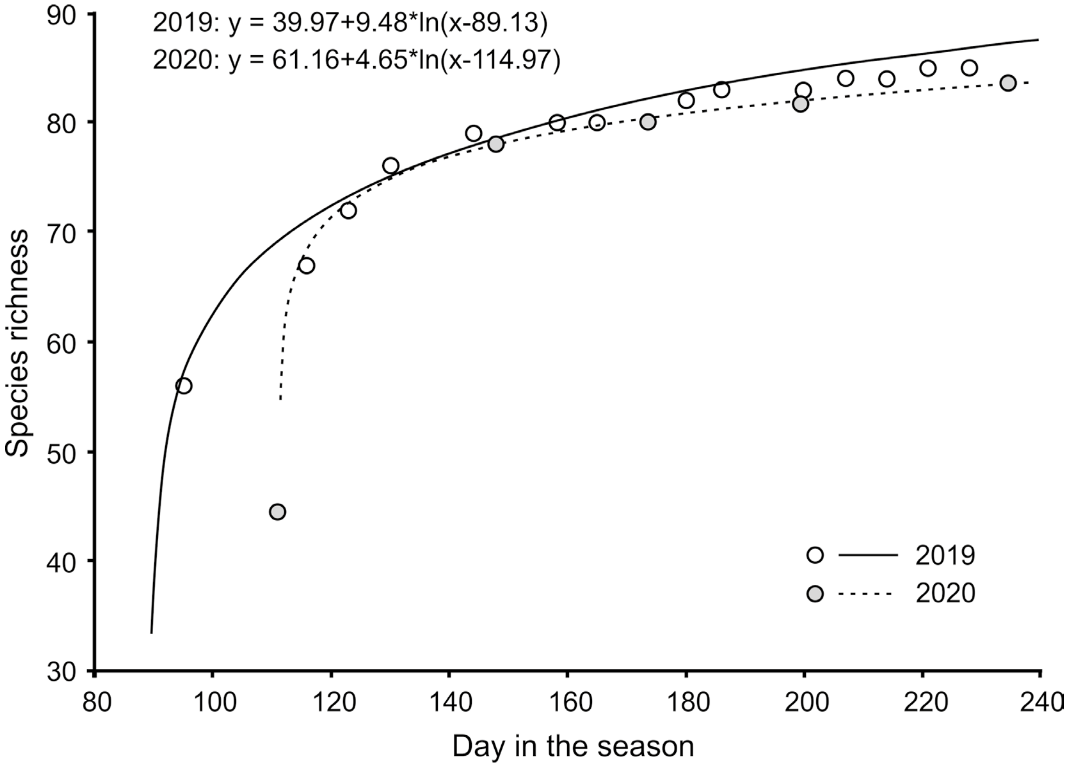

Fig. 2. Cumulative graphs for numbers of recorded species (species richness) during the breeding season (day of the season). Data from 2019 (n = 14 visits) and 2020 (n = 5 visits) are shown separately.

data pooled from both the breeding seasons were calculated using linear regression, but only for species with more than ten records (n = 55 species). For the species that did not show a linear relationship I used non-linear estimation. Non-linear estimation was also used to fit the relationship between Shannon-Wiener diversity index and the day in the season (i.e. Julian day). Potential between-year changes in temperature and aggregate rainfall were calculated using Wilcoxon matched pairs tests based on monthly values from the database www.worldweatheronline.com. All statistical procedures were analysed using Statistica 13 software (TIBCO Software Inc. 2017).

Results

Bird community

In total, I recorded 87 bird species within the transect buffer during the study period. The core of the bird community (> 40 pairs/km^2) was represented by common species, but only the whinchat (*Saxicola rubetra*) is a key species for semi-open mountain habitats in the Czech Republic. Among open-habitat species, increased densities (20-40 pairs/km^2) were recorded for the tree pipit (*Anthus trivialis*). Species of closed habitats with intermediate abundances (10-20 pairs/km^2) were represented typically by coal

Table 1. Mean (2019) and total (2020) numbers of individuals within each category of observation type recorded per month and diversity index within the transect in each year and their comparisons using a Wilcoxon matched pairs test.

Month/year	Adult individuals		Flocks of adults		Juvenile individuals		Diversity index		Mean/total number	
	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020
April	244.0	179.0	84.5	0.0	0.0	0.0	3.755	3.713	328.5	179.0
May	231.7	265.0	16.7	0.0	0.0	0.0	3.854	3.970	248.3	265.0
June	197.0	180.0	6.7	0.0	6.3	0.0	3.856	3.768	210.0	180.0
July	145.0	142.0	0.0	0.0	24.0	121.0	3.842	3.970	169.0	263.0
August	105.3	74.0	0.0	0.0	140.3	140.0	3.654	3.482	245.7	214.0
Z	0.94		-		0.44		0.13		0.67	
P	0.345		-		0.655		0.893		0.500	

tit (*Periparus ater*), red crossbill (*Loxia curvirostra*) and Eurasian bullfinch (*Pyrrhula pyrrhula*). Similar densities were also found of some species of open and semi-open habitats (e.g. corncrake *Crex crex*, common quail *Coturnix coturnix,* common snipe *Gallinago gallinago* and red-backed shrike *Lanius collurio*). The mix of open and closed habitats also hosted low abundances (< 10 pairs/km^2) of other open habitat species (e.g. woodlark *Lullula arborea*) and species of semi-closed and closed habitats (e.g. Eurasian wryneck *Jynx torquilla*, stock dove *Columba oenas* and spotted nutcracker *Nucifraga caryocatactes*). Due to the presence of urban habitats at the beginning of the transect, I recorded increased abundances (> 10 pairs/km^2) of species that are associated with these habitats (e.g. black redstart *Phoenicurus ochruros*, Table S1).

Effect of sampling effort

The cumulative number of detected species showed a similar pattern in 2019 and 2020. However, 80% of species in 2020 were detected around the 170th day of the year (June) while in 2019, the same number of species was reached about ten days earlier (Fig. 2). The total number of bird species recorded within one month differed only marginally between years (Wilcoxon matched pairs test, Z = 1.75, *P* = 0.075). With the exception of May, the monthly number of species in was lower in 2020 than 2019 (Fig. 3a). In

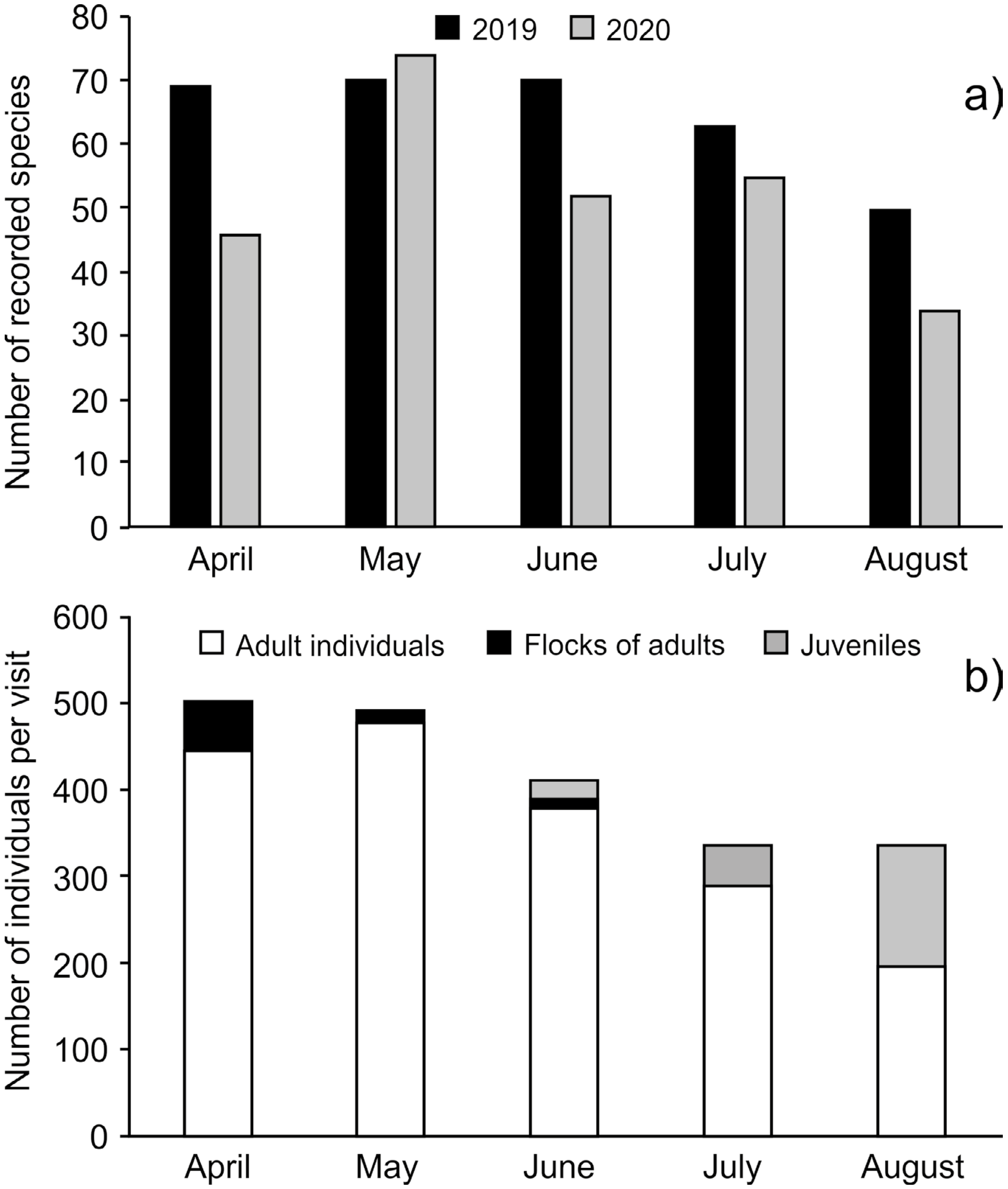

Fig. 3. The (a) number of recorded species within each month of the year 2019 and 2020 and (b) the mean number of individual adult and juvenile birds recorded on the transect in each month of the study (data pooled from the year 2019 and 2020).

contrast, the monthly number individuals did not differ significantly between years (Table 1). I also looked at interannual changes in monthly numbers within observed categories (adult individuals, flocks of adults and juveniles) and mean diversity index. For flocks of individuals, this comparison was not possible due to a lack of flocks in 2020. The analysis did not reveal any interannual differences in monthly numbers of individual adults or juveniles nor in the mean/total number of individuals. Therefore, the presence of some larger flocks in April 2019 did not affect the mean/total number of individuals. Between years there were no differences in mean monthly diversity of the bird community despite its slight decrease in April and August 2020 (Table 1).

Intra-seasonal changes in bird community

For analyses of intra-seasonal changes, the data from both breeding seasons were pooled. The mean diversity of the bird community (mean ± SD) was 3.79 ± 0.12 (min-max, 3.48-3.97). I calculated the minimum diversity values for the beginning and end of the breeding season using data pooled from both study years. The maximum diversity was detected in the middle of the study period (Fig. 4). When I compared the numbers of adult flocks, adult, and juvenile individuals during the breeding season, I found the number of individual adults decreased from April to August. At the same time, I found highest numbers of adult flocks at the beginning of the study period (April), which continually decreased until June and then completely disappeared. I first recorded juvenile individuals in June after which their abundance increased gradually until August (Fig. 3b).

I detected four main relationships between species abundance and the day of the year (Fig. 5). In many species (n = 24), I recorded a significant negative relationship between abundance and the day of the year (Fig. S1-S4). This relationship was most pronounced (beta < –0.60) in Turdidae (song thrush *Turdus philomelos*, common blackbird *Turdus merula*, mistle thrush *Turdus viscivorus*), European robin (*Erithacus rubecula*), goldcrest (*Regulus regulus*), common chaffinch (*Fringilla coelebs*), common starling (*Sturnus vulgaris*), dunnock (*Prunella modularis*), yellowhammer (*Emberiza citrinella*) and black redstart. Interestingly, I recorded the opposite trend in two species (willow tit *Poecile montanus* and European goldfinch *Carduelis carduelis*, Table 2, Fig. S5). In other species I did not find a significant linear relationship (Fig. S6-S7). In most of these species, no relationship was detected (n = 21), but in some species (n = 8), I detected a non-linear trend during the breeding season. In six species (common wood pigeon *Columba palumbus*, red-backed shrike, whinchat, grey wagtail

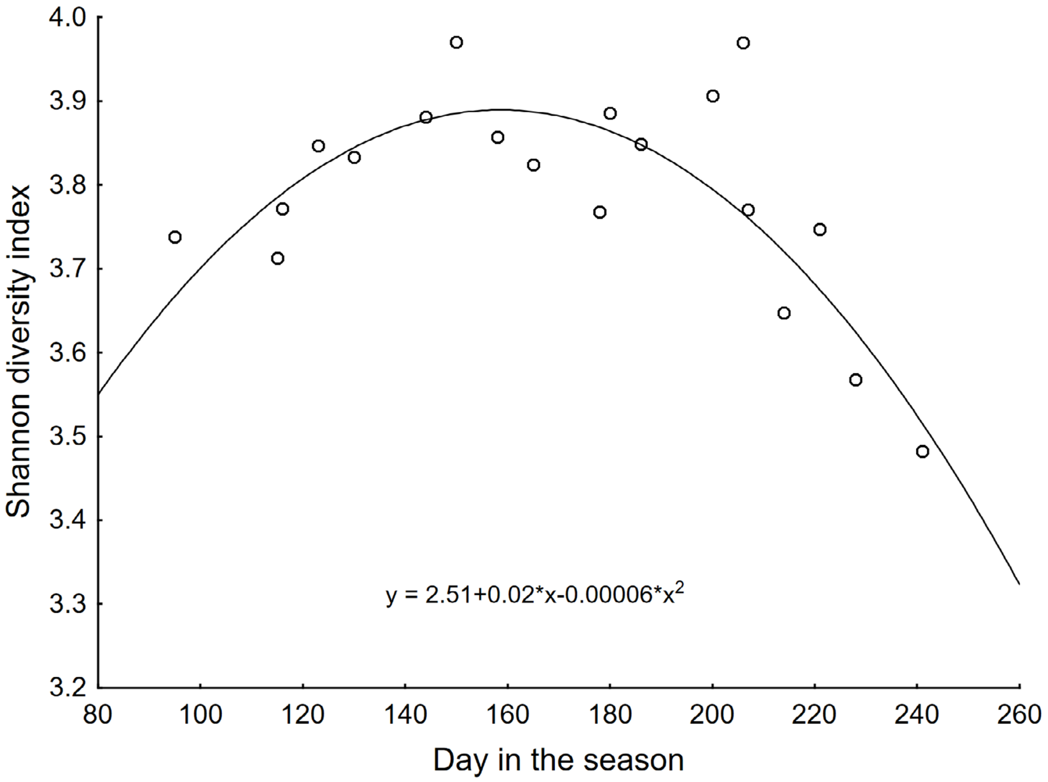

Fig. 4. The relationship between Shannon diversity index of the bird community and day of the season. Data from years 2019 and 2020 (n = 19 visits) were merged. Non-linear estimation, final loss = 0.10, R = 0.80, variance explained = 64.38%.

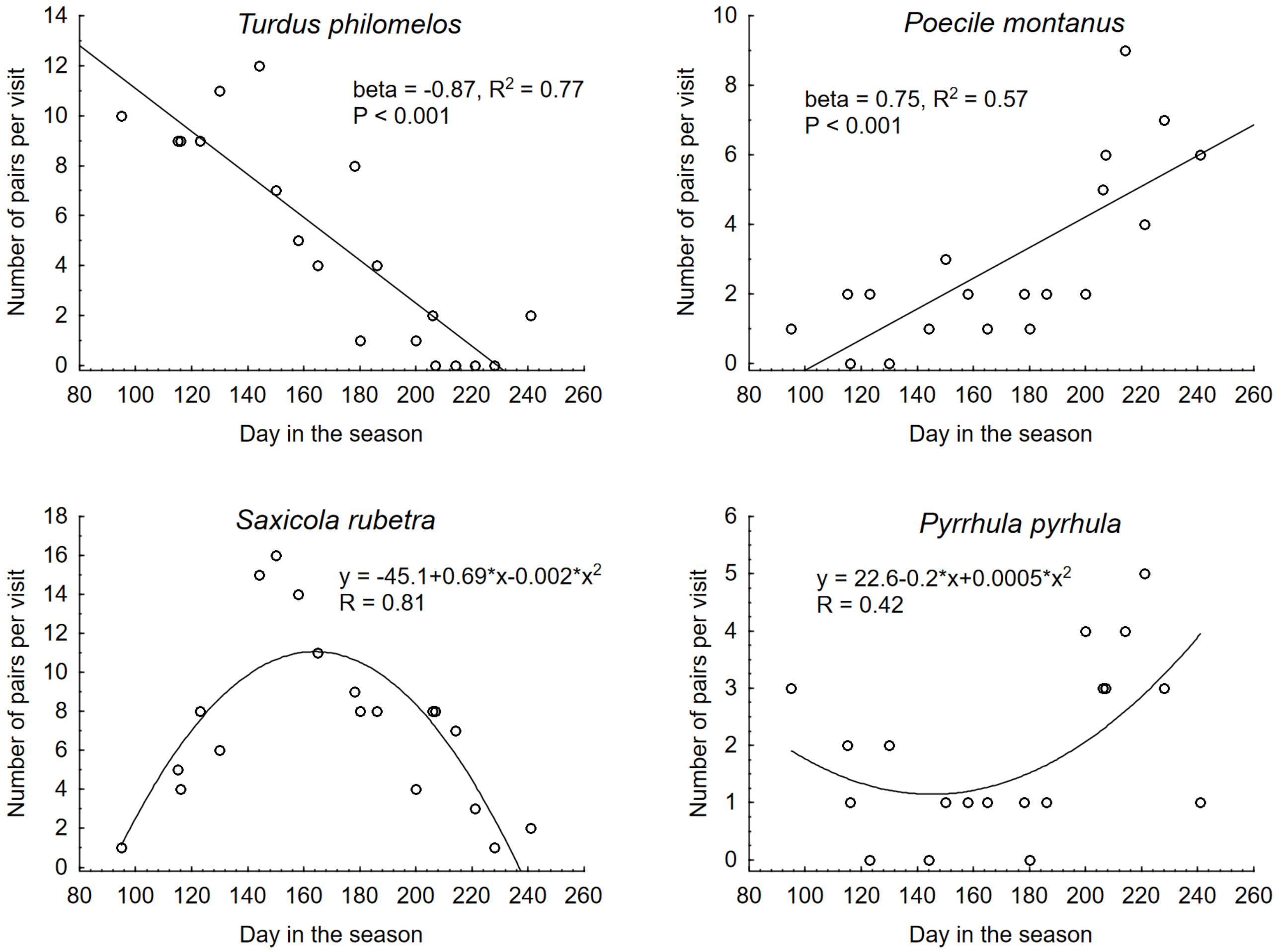

Fig. 5. Examples of four main intra-seasonal trends in abundance of detected pairs within the study area. Decreasing (*Turdus philomelos*) and increasing (*Poecile montanus*) trends were fitted by linear regression. Non-linear estimations were applied for species with peak abundances in the middle (*Saxicola rubetra*) and lowest abundances in the middle (*Pyrrhula pyrrhula*). Only individuals with territorial displays were included, spring flocks of adult birds and summer flocks of juveniles were excluded. For graphs of all species with at least ten recorded pairs within the study period see Fig. S1-S7.

Motacilla cinerea, Eurasian blackcap *Sylvia atricapilla* and common whitethroat *Sylvia communis*), I detected an abundance peak in the middle of the breeding season. In contrast, two species (Eurasian siskin *Carduelis spinus* and Eurasian bullfinch) showed minimum abundance in the middle of the study period.

Discussion

The study area borders the Bohemian Forest National Park, which represents an important refuge area for forest birds in Central Europe (Scherzinger 2006). Therefore, the bird community of the studied transect was highly influenced by the presence of forest species such as the black woodpecker (*Dryocopus martius*), red crossbill, stock dove and spotted nutcracker. On the other hand, the large proportion of open areas along the transect led to increased densities of endangered species such as the corncrake, common quail, red-backed shrike, and whinchat. Simultaneously, the presence of wet meadows attracts other species, such as common snipe, while transitional woodland-shrub areas are occupied by the Eurasian wryneck. Bird community diversity was further enhanced by the presence of urban species. In conclusion, the bird community is highly diversified due to the mosaic of habitats and concurs with a previous study in the same mountains (Scherzinger 2006).

Bird detectability under different sampling effort

Insufficient sampling effort in ornithological studies may be a source of bias (Pendleton 1995, Walther & Martin 2001, Thompson 2002, Watson 2017). In my study, the sampling effort in 2020 was nearly three times lower than in 2019. In contrast, the trend in cumulative number of species during the season was similar in both years. This result partially conflicts with the largely accepted theory that decreased sampling effort necessarily results in decreased estimates of species richness (Schneider 1994, Neave et al. 1997, Walther & Martin 2001). According to Watson (2003),

Table 2. The relationships between species abundance (number of pairs) and day of the season. Regressions were calculated only for species with abundances higher than 10 pairs during the whole study period. Species are ordered according to beta values, from the lowest value to the highest.

Species	Beta	R^2	F	*P*
Turdus philomelos	–0.87	0.77	55.40	< 0.001
Turdus merula	–0.81	0.65	31.59	< 0.001
Regulus regulus	–0.77	0.59	24.72	< 0.001
Turdus viscivorus	–0.77	0.60	25.34	< 0.001
Erithacus rubecula	–0.73	0.54	19.93	< 0.001
Fringilla coelebs	–0.72	0.52	18.35	0.001
Troglodytes troglodytes	–0.70	0.49	16.19	0.001
Sturnus vulgaris	–0.70	0.49	16.03	0.001
Prunella modularis	–0.63	0.40	11.23	0.004
Coccothraustes coccothraustes	–0.62	0.38	10.57	0.005
Emberiza citrinella	–0.62	0.39	10.89	0.004
Regulus ignicapillus	–0.61	0.38	10.18	0.005
Phoenicurus ochruros	–0.61	0.37	9.82	0.006
Phylloscopus collybita	–0.58	0.33	8.55	0.009
Passer domesticus	–0.58	0.33	8.43	0.010
Anthus trivialis	–0.58	0.33	8.49	0.010
Cyanistes caeruleus	–0.56	0.31	7.61	0.013
Phylloscopus trochilus	–0.56	0.32	7.83	0.012
Turdus pilaris	–0.55	0.30	7.33	0.015
Motacilla alba	–0.54	0.30	7.10	0.016
Certhia familiaris	–0.53	0.28	6.67	0.019
Parus major	–0.50	0.25	5.80	0.028
Periparus ater	–0.48	0.23	5.19	0.036
Loxia curvirostra	–0.45	0.20	3.28	0.084
Carduelis chloris	–0.44	0.19	3.99	0.049
Columba palumbus	–0.42	0.18	3.75	0.076
Streptopelia decaocto	–0.41	0.17	3.52	0.078
Sylvia atricapilla	–0.37	0.14	2.68	0.120
Phoenicurus phoenicurus	–0.36	0.13	2.55	0.129
Sylvia communis	–0.33	0.11	2.02	0.173
Carduelis spinus	–0.33	0.11	2.09	0.166
Oriolus oriolus	–0.30	0.09	1.69	0.211
Passer montanus	–0.29	0.09	1.61	0.222
Motacilla cinerea	–0.25	0.06	1.17	0.295
Dryocopus martius	–0.23	0.05	0.95	0.343
Alauda arvensis	–0.21	0.04	0.78	0.390
Aegithalos caudatus	–0.21	0.04	0.76	0.394
Muscicapa striata	–0.21	0.05	0.81	0.382
Sylvia borin	–0.20	0.04	0.74	0.401
Saxicola rubetra	–0.19	0.04	0.66	0.427
Locustella naevia	–0.14	0.02	0.35	0.562
Acrocephalus palustris	–0.06	< 0.01	0.06	0.805

Table 2. continued.

Species	Beta	R^2	F	*P*
Coturnix coturnix	–0.02	< 0.01	0.01	0.931
Crex crex	0.07	< 0.01	0.07	0.790
Lophophanes cristatus	0.13	0.02	0.31	0.586
Anthus pratensis	0.14	0.02	0.32	0.578
Gallinago gallinago	0.18	0.03	0.31	0.586
Dendrocopos major	0.23	0.05	0.96	0.341
Garrulus glandarius	0.28	0.08	1.41	0.253
Lanius collurio	0.31	0.10	1.80	0.198
Hirundo rustica	0.31	0.09	1.75	0.203
Sitta europaea	0.35	0.12	2.36	0.143
Pyrrhula pyrrhula	0.42	0.17	3.58	0.075
Carduelis carduelis	0.44	0.20	4.11	0.047
Poecile montanus	0.75	0.57	22.3	< 0.001

the effort-stopping rule for bird monitoring may be applied when the ratio of singletons (species detected only in one sampling period) to doubletons (species detected in two sampling periods) is ≤ 1.2. In my dataset, the ratio of singletons to doubletons was 1.17 in 2019 and 0.65 in 2020. Both the values were below the proposed critical value and the proportion of singletons to doubletons was even higher in the year with greater sampling effort. This was probably caused by the similar trend in cumulative curves for both years. The only marked difference was that 80% of species recorded in 2019 was reached ten days earlier than in 2020 and was probably caused by more intensive sampling in 2019 compared to 2020.

I recorded a marginally significant decrease in numbers of monthly recorded species in 2019 compared to 2020. However, the monthly numbers of individuals and diversity did not change significantly between the years despite of slight decrease in diversity in April and August 2020. These results may also indicate that increased sampling effort may enhance the detectability of species (Neave et al. 1997) but does not influence the reliability of population size estimates. However, it is important to note that in both years I conducted at least five consecutive bird surveys at regular intervals, which may be sufficient to uncover real population sizes (Bibby et al. 2000, Walther & Martin 2001). During the breeding season, I recorded an increased proportion of flocks of adult birds in the beginning of the 2019 season (April) and an increased proportion of juvenile individuals at the end of the season in both years (July-August). The absence of flocks of adult individuals in 2020 was probably caused by decreased sampling effort. The total monthly numbers of individuals within other categories (adult and juvenile individuals) did not differ between the years indicating that the sampling effort was sufficient in both years.

Bird detectability during the breeding season

I recorded a peak of bird community diversity in the middle of the sampling period (May-July). An increase of bird species diversity from winter to spring has also been recorded in other studies, explained by the arrival of migratory species from their wintering areas (Rotenberry et al. 1979, Avery & van Riper 1989, Isacch et al. 2003, Lorenzón et al. 2019, Yabuhara et al. 2019). The decrease in diversity in late summer (August) can be explained by decreased song activity for most species at the end of the breeding season, which is connected to other activities, such as caring for fledged young (Slagsvold 1977). Further, I investigated the seasonal changes in number of individuals and pairs detected for each species (n = 55 species) in detail. The species were subsequently divided into five groups: 1) species with no trend (38.2%), 2) species with decreasing trend (43.6%), 3) species with increasing trend (3.6%), 4) species with a peak in the middle of the sampling period (10.9%), and 5) species showing minimum values in the middle of the sampling period (3.6%).

Most species (> 80%) showed either a decreasing trend or no trend. Some non-migratory species of the families Paridae and Passeridae, for example, showed a decreasing trend. However, most species with a decreasing trend were migratory species arriving in early spring (Turdidae, Muscicapidae, Prunellidae, Motacillidae, Sturnidae, Fringillidae and Emberizidae; Cepák et al. 2008). In general, the decreasing trend can be explained by an increased proportion of nesting activities at the end of the breeding season (Slagsvold 1977).

Interestingly, in two species (European goldfinch and willow tit) I recorded increasing trends. It is important to note that flocks of young and adult birds were not included in the analysis. There may be various reasons why detectability (i.e. song activity) of these species increased at the end of the breeding season. In most species, during autumn, fully grown young from the preceding breeding season start to sing (Marler & Slabbekoorn 2004). Willow tits have a rather simple song (Šťastný & Hudec 2011) that is probably inherited from their parents, like other passerines with simple songs, such as the Eastern phoebe *Sayornis phoebe* (Kroodsma & Konishi 1991). Therefore, the singing of juvenile willow tits probably occurs early after leaving the nest. A similar explanation can be applied to the European goldfinch, but its song is much more elaborate compared to the willow tit's (Šťastný & Hudec 2011). Unfortunately, the age at which young European goldfinches start to fully sing is unknown. Another explanation may be an identical proportion of day to night during the spring and autumn equinox. The breeding season in the temperate zone starts when the nights get shorter; shorter nights induce increased levels of gonadotropin-releasing hormone, causing the development of follicles in females and increased testosterone levels in males, increasing song activity (reviewed by Dawson et al. 2001). Due to the similarity in proportion of day to night, there is also an increase in the size of song control nuclei (HVC and RA), although their size is much smaller in autumn compared to spring (Brenowitz et al. 1991, Nottebohm 2004). Consequently, due to the change in size of the song control nuclei caused by different proportions of day and night, at least some adult individuals may produce their songs in autumn as well as in spring (Whitfield-Rucker & Cassone 2000). I suggest that these two factors together might cause the increased detectability of both species during the late summer.

In several species, I detected a peak in the middle of the breeding season. With the single exception of the common wood pigeon, these species were migratory and dependent on the availability of invertebrate prey (red-backed shrike, whinchat, grey wagtail, Eurasian blackcap, common whitethroat). Therefore, it is reasonable to suggest that the increased detectability from spring to summer was caused by the gradual arrival of individuals from wintering areas. The decrease in detectability at the end of summer can be attributed to activities connected with reproduction. In contrast, two species (Eurasian siskin and Eurasian bullfinch) showed their minimum detectability in the middle of the breeding season. This result is in contrast with a previous study (Slagsvold 1977) showing that, except for the Eurasian bullfinch, there was a decreasing trend in song activity during the breeding season. Since the songs of both the species are rather quiet (Šťastný & Hudec 2011), I suggest that during the breeding season their songs can be easily obscured by the much louder songs of other species. In the Eurasian bullfinch, it has also been observed that, during the late summer, it significantly increases its habitat breadth (Alatalo 1981), making the species more conspicuous during this period due to the decreased vocalization of other species.

In conclusion, sampling effort influenced the monthly numbers of species detected, but the overall estimate of species numbers for the whole breeding season was not greatly affected. I also did not find significant differences in monthly diversity values of the bird community. Sampling effort marginally, yet significantly affected the recorded monthly numbers of bird individuals. These results were probably caused by the fact that even the lower sampling effort was still sufficient to detect the true bird community structure, showing a peak in diversity in the middle of the study period. I recorded different trends in detectability among different species over the course of the breeding season. Migratory species often showed a decreasing trend or a peak in the middle of the breeding season. I also recorded some increasing trends that can be explained by song activity of juveniles or late summer song activity of adult individuals.

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Data Availability Statement

The data that support the findings of this study are available in the FigShare Digital Repository under the name "primary data.xlsx": http://dx.doi.org/doi:10.6084/m9.figshare.19941338.

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Supplementary online material

Table S1. Maximal densities of breeding bird species detected along the road from Přední Zvonková to the border crossing Zvonková/Schöneben. Species are ordered from the highest to the lowest densities.

Fig. S1. Trends in detectability of bird species at the transect from Přední Zvonková to border with Austria (Czech Republic). Results of regression analyses are available in Table 2.

Fig. S2. Trends in detectability of bird species at the transect from Přední Zvonková to border with Austria (Czech Republic). Results of regression analyses are available in Table 2.

Fig. S3. Trends in detectability of bird species at the transect from Přední Zvonková to border with Austria (Czech Republic). Results of regression analyses are available in Table 2.

Fig. S4. Trends in detectability of bird species at the transect from Přední Zvonková to border with Austria (Czech Republic). Results of regression analyses are available in Table 2.

Fig. S5. Trends in detectability of bird species at the transect from Přední Zvonková to border with Austria (Czech Republic). Results of regression analyses are available in Table 2.

Fig. S6. Trends in detectability of bird species at the transect from Přední Zvonková to border with Austria (Czech Republic). Non-linear estimation analyses.

Fig. S7. Trends in detectability of bird species at the transect from Přední Zvonková to border with Austria (Czech Republic). Non-linear estimation analyses.

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